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Lightweight Corer Designed for Sampling Very Soft Sediments

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WILLIAMS, J. D. H., AND A. E. PASHLEY. 1979. Lightweight corer designed for sampling very soft sediments. J. Fish. Res. Board Can. 36: 241–246.

An underwater corer has been developed capable of taking 10-cm diam cores up to 1 m long from unconsolidated, fine-grained fluvial and lacustrine sediments including organic-rich (gyttja-like) deposits. The corer is lightweight and compact for transport and hand operation from float planes and small boats. It is of the piston type and has a sphincter valve for core retention. A miniature optical sensor triggers the corer when the sediment–water interface is penetrated. The corer is compatible with a system to subdivide the cores by vertical extrusion.

Key words: corer, sediment, piston, sampling

WILLIAMS, J. D. H., AND A. E. PASHLEY. 1979. Lightweight corer designed for sampling very soft sediments. J. Fish. Res. Board Can. 36: 241–246.

On a mis au point un carottier sous-marin capable de prélever des carottes de 10 cm de diamètre et de longueurs allant jusqu'à 1 m de sédiments fluviaux et lacustres non consolidés et à grain fin, y compris des dépôts riches en matière organique (ressemblant à un gyttja). Léger et compact, le carottier est facile à transporter et peut être actionné à la main d'un flotteur d'avion ou d'une petite embarcation. Il est du type piston et est muni d'une soupape à sphincter servant à retenir la carotte. Un détecteur optique miniature déclenche le carottier au moment où ce dernier atteint la surface du sédiment. Il peut très bien s'intégrer dans un système en vertu duquel les carottes peuvent se subdiviser par extrusion verticale.

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LAKE sediment cores have long been studied in investigations of climatic, vegetational, and other changes during the Holocene period. Techniques for obtaining such cores have been reviewed by Wright et al. (1965). More recently, investigations of the topmost part of the sediment column, representing the material deposited during the last few hundred years, have been a feature of many geoexploration, limnological, geochemical, and environmental studies. Interest has focused on such topics as changing inputs of nutrients, exotic organic compounds and radionuclides, and the migration of many elements from reduced to oxidized regions of the sediment column.

Problems are still encountered, however, in obtaining undisturbed representative cores of very soft sediments from small lakes, especially those that do not provide firm ice platforms for wintertime sampling. The commercially available Benthos (Benthos, Inc., Edgerton Drive, North Falmouth, MA 02556, USA) gravity corer and a specific modification, the Triple Benthos corer (Kemp et al. 1971), have proved entirely

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adequate for the softer types of sediment encountered in the Great Lakes, on which large vessels can be used. We have found that these corers do not perform so well in the highly fluid, frequently organic, sediments found in many small lakes, notably in the Canadian Shield. The corers are too heavy for easy hand use from small boats, and cores of very soft sediments are apt to slide out of their liners during ascent through the water. Lightweight pistonless gravity corers with barrels <5-cm inside diameter (ID), such as the Phleger and Kajak–Brinkhurst corers (Phleger 1951; Brinkhurst et al. 1969) recover short cores (typically 20–30 cm long) from soft sediments. The narrow diameter limits the amount recovered; thus, for a sediment of 95% water content, common for organic sediments, a 1-cm long section of a 5-cm diam core contains only 1 g of solids. Further, the greater ratio of area of barrel wall to volume of core for the narrow corers increases the tendency for core shortening to occur due to friction between mud and core barrel. An example of core shortening using the Phleger corer is discussed below. A possible additional danger is that in very soft sediments any type of corer activated by the mechanical resistance of the sediment may penetrate to a depth greater than the length of the core barrel, displacing part of the core through the top of the barrel. Such an effect might not be easily detectable if core slippage occurred during the subsequent ascent through the water column.

This paper describes a lightweight corer, developed for the small lakes program of the Department of Fisheries and the Environment, in which these and other difficulties have been reduced or overcome.

Criteria of the Corer Design

The following criteria, an extension of those listed by Menzies and Rowe (1968), were established for the design and evaluation of a corer intended primarily for recovering short cores of very soft sediments for geochemical studies:

1) ability to sample the most fluid sediments, including gyttja of high organic matter content;
2) a standard core length of 1 m;
3) easy adaptability for taking cores of other lengths;
4) operation in water depths of 100 m or more;
5) minimal disruption of the interface;
6) arrest of the descent of the corer after it has penetrated the sediment of a depth equal to the length of the core barrel;
7) no core compaction during penetration;
8) no loss of core from the barrel during retrieval;
9) a greater internal diameter than that of the Benthos corer (6.7 cm) so as to increase subsample weight for a given thickness of sediment;
10) stable vertical orientation on descent and entry into the sediment column;
11) rapid triggering at the moment of entry into the sediment column even in the most fluid sediments;
12) compact, lightweight, sturdy, corrosion-resistant construction for hand operation from a variety of unmoored sampling platforms such as small boats, canoes, float planes, or helicopters;
13) fully automatic triggering with one support line only and no platform-borne ancillary equipment such as the compressed air source required by the corer of Mackereth (1958);
14) easy assembly and disassembly on any type of sampling platform;
15) compatibility with the vertical extrusion technique for subdividing cores (Kemp et al. 1971; Williams and Pashley unpublished data).

It is acknowledged here that any corer meeting these requirements would be unable to penetrate stiff substrates such as glacial tills, sandy deposits, etc.

Criteria 6 and 7 are met by piston corer designs (Emery and Hulsemann 1964; see also Ross and Riedel 1967). To meet criteria 8 and 9, a core-retaining device is essential. In our experience, "core catchers," passive retaining devices placed inside core liners (Bouma 1969), disturb the sediment–water interface unduly. Active retaining devices, triggered by the corer after completing its descent through the sediment, are a feature of several corer designs (Ambühl 1969; Craib 1965; Kajak 1969; Mills 1961; Mortimer 1942; Pamatmat 1971). The most elegant device to date is the sphincter valve (Kermabon et al. 1966; Burke 1968). As well as being simple in form, it has minimal cross-sectional area in the direction of descent. This minimizes resistance to sediment penetration and reduces disruption of the sediment–water interface.

Several systems that depend on the mechanical resistance of sediments have been devised for trigggering piston corers (Davis and Doyle 1969; Isaacs and Brown 1968; Kermabon et al. 1966). We felt that these triggering systems would not function reliably in highly fluid sediments. Instead, this corer incorporates a novel electronic sensing device that triggers the corer when light is cut off as the sensor enters the sediment.

Description of Corer

The corer, illustrated in Fig. 1, consists of a sphincter/cutter assembly, core barrel, piston/valve assembly, triggering system, corer head, support and safety lines, and tie rods. With a nominal 1-m long core barrel, the corer mass is 13 kg and its overall length is 2 m. Cost of fabrication is of the order of a few thousand dollars.

Sphincter/Cutter Assembly

This unit fits over the lower end of the core barrel and is sealed by an O-ring. Its major components are a tapered cutting edge with a 101-mm ID, and a nylon fabric sphincter valve that can open and close by rotating on a Teflon® bearing. A sphincter line joins the valve to a bridle around the piston line. The bridle can slide freely along this line until checked by the boss at its lower end. In the assembled position the bridle rests under the trigger bar in the corer head. A lead collar surrounds the sphincter/cutter assembly to give the desired corer weight. This also lowers the center of gravity of the corer, helping it to maintain a vertical orientation while penetrating the sediment column.

Core Barrel

This component is made from cellulose–butyrate–acetate tubing with a 101-mm ID and 3.3-mm wall thickness. The nominal 1-m long tube is made in two pieces, 0.06 and 1.33 m long; these are joined together by a single wrap of bookbinding tape. This joint is placed at the lower end of the corer. Its function when dismantling the corer after retrieving a core is described below.

Piston/Valve Assembly

The piston has an elastomer lip seal around its circumference. It has a large diameter spring-loaded valve to vent through the piston. Normally, this spring-loaded valve is open so that when only a partial core is obtained, the piston can be slowly pulled to the top of the core barrel without disturbing the core material below the piston. This valve is automatically closed when the piston reaches the top of the core barrel. During the rapid drop of the corer into the sediment, the valve slams shut because of differential pressure, and the piston then acts as though it is solid. Also venting through the piston is a small, positive-seal valve. This is normally closed, and is only opened to break the suction when removing the piston from the top of the core barrel. Three different lever devices are built into the piston. The first device holds the lower end of the piston line. It releases the line only when the piston reaches the top of the core barrel. The second device holds the large, spring-loaded valve closed while the piston is at the top of the core barrel. This prevents loss of core material when the corer is removed from the water. These two devices are mounted on the same tripping lever. The third lever system automatically clamps the piston to the corer head when the piston is at the top of the core barrel — this lever can be released manually during the core barrel removal.

Triggering System

The triggering system is powered and controlled by the electronic control package, which consists basically of a rechargeable battery, a large capacitor, and oscillator and logic circuitry housed in a waterproof canister in the corer head Flotation chambers attached to the canister keep the corer vertically oriented in water. The mud sensor is attached to a bracket on the sphincter/cutter assembly, and consists of a light emitting diode (LED) and a photo transistor housed in a waterproof acrylic casing. The oscillator generates pulses of light from the LED at roughly 0.1-s intervals to minimize battery drain. When the current from the photo transistor (due to ambient light and/or the LED) falls below a certain value, the logic circuitry allows the large capacitor to energize a rotary solenoid for 0.5 s.

Corer Head

This consists of a light aluminum framework at the top of the corer forming a protective cage for easy and safe handling of the corer. It carries the electronic control package and the solenoid housing. An aperture in the head fits over the upper end of the core barrel which is sealed by an O-ring. Above the core barrel is a slotted and hinged trigger bar through which the piston line passes. The trigger bar is locked in a horizontal (cocked) position by the solenoid lever when the solenoid is unenergized. Rotation of the lever allows the bar to pivot into a vertical (released) position when the solenoid is energized.

Lines and Rods

The sphincter line has already been described. Two consecutive lines support the corer. The piston line is a thin stainless steel wire rope that lies within the corer when cocked. A 2-cm diam boss at its lower end links the line to the piston via the tripping lever. The line is strung with metal beads totalling 1 m in length. In the cocked position, these beads become rigid under the tension of supporting the entire weight of the corer, with the ends of the chain against the boss and the underside of the trigger bar. They thus prevent the piston from sliding up the core barrel when lowered through the water. The distance traveled by the piston at the moment of coring, and hence the length of core recovered, can be adjusted, if required, by moving some of the beads above the trigger bar. Above the corer, the support line consists of a polypropylene rope linked to the piston line by a shackle. This rope is marked off in meters. This enables the corer to be lowered very slowly near the sediment interface, so that the triggering of the corer can be felt by holding the line.

A safety line is attached to the same shackle and to the protective cage of the corer head. Two tie rods rigidly couple together the corer head, core barrel and the sphincter/cutter assembly.

Operation of Corer

The assembled corer is shown in Fig. 1. The sphincter is opened to its maximum extent and the corer is armed by inserting an arming plug containing a built-in resistor into the electronic control package. This starts the LED flashing. It also starts the charging of the capacitor, a process that is complete after ~90 s. When the mud sensor enters the sediment, light pulses from the LED no longer reach the photo transistor. This results in the solenoid lever rotating after a delay of ~0.3 s (assuming the capacitor is fully charged). Because of this delay, and to eliminate interface disturbance due to piston movement, a gap of ~0.3 m separates the piston from the sphincter valve. Due to the pressure of the beads on the piston line, the released trigger bar swings upwards out of the way of the line, and the entire corer (except for the stationary support lines and piston) drops under its own weight into the sediment. The entry of sediment into the core barrel is stopped either by the

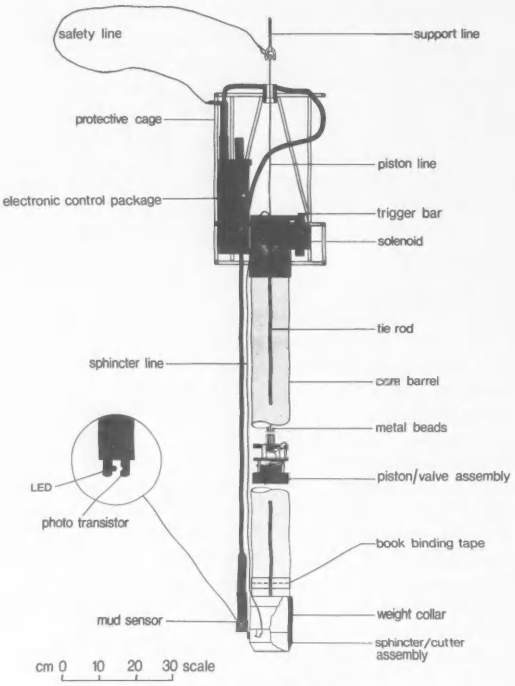

FIG. 1. Diagram of the corer.

corer coming to rest due to the increasing resistance of the sediment or by the piston locking itself into the corer head.

The jerk when the corer is triggered and drops into the mud is felt on the hand-held line; it is difficult to sense only if water depth is >100 m or so. After waiting a few seconds for the corer to complete its descent into the mud, the hand line is gently pulled upwards. This pulls the piston into the corer head, if it has not already done so. The top of the core barrel remains sealed by the piston O-ring. Further hauling detaches the piston line from the piston. Once the bridle reaches the boss on the end of the piston line, the sphincter line is drawn taut and the sphincter valve closed. An experienced operator can sense the separate stages. The entire corer can now be hauled bodily upwards.

When the corer is on board, it is held upright while the tie rods are removed, the sensor and cable detached from the sphincter/cutter assembly, and the sphincter and piston lines uncoupled. The positive-seal screw valve in the piston is then opened and the corer head plus piston lifted off the core barrel, which is then capped and taped.

The top section of the core barrel, while still kept upright, is then separated from the sphincter/cutter assembly at the junction of the two core barrel pieces by means of a special cutter plate. This cutter has a

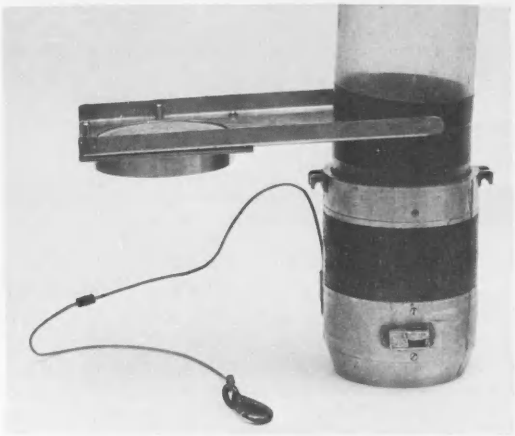

FIG. 2. Core cutter slicing through tape over joint in the core barrel, before positioning a sealing plug in the bottom of the barrel.

dual role. Firstly, it cuts through the layer of tape around the core barrel; secondly, it positions a plug under the top section of the core barrel so that the barrel is now effectively sealed at both ends. This operation is shown in Fig. 2. The bottom end of the upper core barrel is then capped and taped, and the core stored vertically until ready for subdivision by vertical extrusion. All sediment between the joint of the core barrel and the cutting edge of the sphincter/cutter assembly is normally discarded. As this amounts to a depth of about 20 cm of sediment, a prerequisite for successful coring is a sediment column at least 30 cm or so deep.

Results with Corer

To date, the corer has recovered over 60 cores in water depths ranging up to 140 m. It has successfully recovered 1-m cores from locations where sediment consistency, at a depth of 20 cm below the interface, varied from 0.15 to 1.4 $kN \cdot m^{-2}$, measured as described by Terzaghi and Peck (1967, p. 347). Recovered sediment cores with tubificids in place at the interface indicate that the corer causes little disturbance of the sediment–water interface, even where the consistency of the material was <0.05 $kN \cdot m^{-2}$. The upper limit of sediment consistency in which the corer can still function is not known, but it is interesting to note that on one occasion the corer recovered a longer core than did a much heavier commercial Benthos corer.

The corer has been successfully operated from small (3-m) boats and from a DAC Beaver float plane. Several cores can be taken on a single flight. The time required on station for measuring water depth, obtaining a grab sample of the sediment, lowering and recovering the corer, separating the core barrel, and

setting up the corer for the next station averaged 20–25 min where water depth did not exceed 20 m.

Excellent cores have also been obtained through the ice on lakes in Manitoba and Saskatchewan, under severe conditions of −32°C and 40 km/h winds. The only alterations to the normal coring techniques are that the corer temperature must be above 0°C before insertion through the ice, the corer must be warmed to thaw it out completely before disassembly and core extrusion, and the corer (especially the sphincter) must be thoroughly dry before attempting another core drop.

Because the corer is lightweight and must enter the sediment vertically, drifting by the sampling platform due to wind or currents creates problems. If drifting is not too severe, the procedure followed has been to lower the corer to within about 3 m of the bottom, maneuver the sampling platform until it is upwind of the corer, then allow the platform to drift. When the platform is almost directly above, the corer is lowered the rest of the way to the bottom.

The degree of light extinction required to trigger the corer in aqueous media was investigated. The corer did not trigger when the mud sensor was immersed in standard Formazin suspension with a turbidity of 4000 Jackson Turbidity Units (Lively 1974). A range of suspensions was created by mixing dark-colored, fine-grained Hamilton Harbour sediment with water. The critical level of turbidity at which the corer triggered lay between 2.6 and 4.1 g of suspended solids per litre of water, using a standard resistance of 360 kΩ in the arming plug. Substituting a 1 MΩ resistance reduced the critical turbidity level to 1.6–2.0 g solids/L. Water sufficiently agitated to support such levels of turbidity is much too energetic to permit deposits of fine-grained sediment to accumulate on the bottom, and even the most fluid sediment has a concentration at the interface of at least 20 g/L, in our experience. The triggering mechanism should, therefore, reliably distinguish between water and sediment in all locations where coring is possible.

The quality of core retrieved by the lightweight corer was compared with cores obtained by three other methods. The deepest part of Conesus Lake, New York, was chosen as the coring location, using an ice platform. The core retrieved by hand coring by scuba diver was taken as the reference core because the core barrel is inserted very gently into the mud, and the entire operation is observed by the diver. Two other corers were also compared, a Phleger corer (Phleger 1951) with a 3.5-cm ID barrel, and a Triple Benthos corer (Kemp et al. 1971) with three 6.7-cm ID barrels. The lengths of the cores recovered by the diver, lightweight, Phleger, and Triple Benthos methods were 44, 43, 22, and 11 cm, respectively. The total carbon values for 1- and 2-cm sections of these cores (Fig. 3) show that down to about 20 cm, the diver and lightweight profiles were very similar, notably in a region 11 cm long where the total C values were consistently <3%. At depths >40 cm below the interface, the total C values increased to more than 5%. In the Phleger core, however, this same increase occurred at an apparent depth of only 20 cm or so below the interface; furthermore, the region where the values were consistently <3% was only 6–7 cm long. This indicates that severe core shortening occurred in the Phleger core, accounting, at least in part, for its shorter length. The region of values <3% was only 5 cm long in the Triple Benthos core. Core shortening here may have been due, in part, to the type of spring-loaded valve used. A commercial Single Benthos corer was not tested because its length and weight make it unsuitable for operation from small boats. It is clear that of the corers tested, the lightweight corer gave total C profiles closest to the diver-taken core.

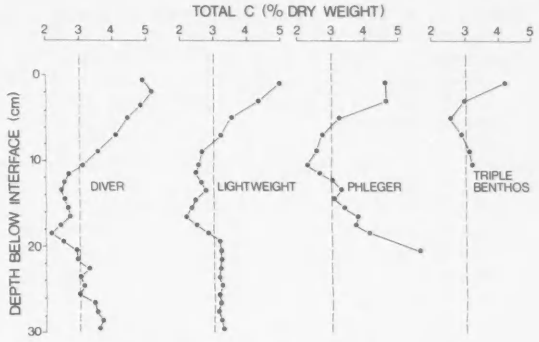

FIG. 3. Comparison of total carbon profiles for four cores from the deepest part of Conesus Lake, New York State. Cores taken by diver, lightweight corer, and Phleger and Triple Benthos corers.

The characteristic features of this corer, notably the sphincter valve and the triggering device, give it several advantages, including larger sample size and absence of core shortening, over other types of lightweight corer. The corer will operate under conditions that preclude a diver, especially great water depths. Under moderately calm conditions, the corer will recover cores from unconsolidated deposits, provided they are at least 30 cm or so thick, in such locations as lakes, reservoirs, lagoons, harbors, and estuaries.

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Uptake from Seawater and Clearance of *p,p'*-DDT by Marine Planktonic Crustacea[1]

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HARDING, G. C. H., AND W. P. VASS. 1979. Uptake from seawater and clearance of *p,p'*-DDT by marine planktonic crustacea. J. Fish. Res. Board Can. 36: 247–254.

A simple exponential model is used to interpret the simultaneous uptake and clearance of *p,p'*-DDT by euphausiids and copepods to and from seawater,

$$\frac{d[C]}{dt} = k_t[W] - k_j[C],$$

where $[C]$ and $[W]$ are the concentrations in the organism and seawater, respectively. The clearance rate constant for euphausiids, $k_j = 0.043$/d, is not significantly different from that observed for copepods, 0.048/d. No trend in k_t values is detected over the range of *p,p'*-DDT concentrations in seawater used, 27.8–1388 ng/L. Furthermore, there is a great deal of overlap in the uptake rate constant values between organisms. Uptake rate constants range from 0.76 to 1.21×10^4/d for euphausiids and from 1.04 to 2.51×10^4/d for copepods. There appears to be no need to use a surface-area term if the concentration of *p,p'*-DDT in the organism is expressed per unit dry weight even though the euphausiids are 2 orders of magnitude larger than copepods. Knowing levels of ΣDDT present in planktonic crustaceans in nature, back calculations suggest that there must be ≪0.1 ng ΣDDT/L in seawater. A considerable amount of the ΣDDT reported in seawater must therefore be unavailable to plankters because it is "bound" to particles.

Key words: *p,p'*-DDT, uptake, clearance, surface area, euphausiids, copepods

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Les auteurs utilisent un simple modèle exponentiel pour interpréter l'absorption et la clairance simultanées de *p,p'*-DDT par les euphausides et les copépodes en direction et en provenance de l'eau de mer,

$$\frac{d[C]}{dt} = k_t[W] - k_j[C],$$

où $[C]$ et $[W]$ représentent les concentrations dans l'organisme et l'eau de mer respectivement. La constante de vitesse de clairance pour les euphausides, $k_j = 0{,}043$/jour, ne diffère pas sensiblement de celle observée chez les copépodes, 0,048/jour. On n'a pas détecté de tendance dans les valeurs de k_t sur la gamme des concentrations de *p,p'*-DDT dans l'eau de mer utilisée, 27,8 à 1 388 ng/L. En outre, il y a beaucoup de chevauchement des constantes de taux d'assimilation d'un organisme à l'autre. Les constantes de taux d'absorption sont comprises entre 0,76 et $1{,}21 \times 10^4$/jour pour les euphausides et entre 1,04 et $2{,}51 \times 10^4$/jour pour les copépodes. Il ne semble pas nécessaire d'utiliser un terme de superficie si la concentration de *p,p'*-DDT dans l'organisme est exprimée en unités de poids sec, même si les euphausides sont de deux ordres de grandeur plus gros que les copépodes. Quand on connaît les niveaux de ΣDDT présents dans les crustacés planctoniques dans la nature, des rétrocalculs donnent à penser qu'il doit y avoir ≪0,1 ng ΣDDT/L dans l'eau de mer. Il faut donc qu'une quantité considérable du ΣDDT signalé dans l'eau de mer soit non accessible aux planctontes parce que «lié» aux particules.

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THERE are numerous studies on the flux of organochlorines between aquatic organisms and water (e.g. Addison 1976; Courtney and Langston 1978; Guiney et al. 1977; Langston 1978). Some authors have attempted to describe their experimental results with kinetic equations (Branson et al. 1975; Harding and Vass 1977; Södergren and Svensson 1973) which could then be used to model pollutants in the aqueous environment (Hassett and Lee 1975; Kerr and Vass 1973; Robinson 1967). In a previous paper we found that the uptake and clearance of *p,p'*-DDT (2,2,-bis-*p*-chlorophenyl-1,1,1-trichloroethane) by a calanoid copepod could be adequately described by a simple exponential model (Harding and Vass 1977). We reasoned that the exposed surface area of an organism should be important in the uptake process although we presented no evidence for this in the paper. To evaluate the importance of surface area and to extend the predictive capability of our model we have repeated the experiments with a larger planktonic crustacean. In the following, we describe the uptake of ^{14}C-*p,p'*-DDT from seawater at four concentrations by a euphausiid shrimp and its clearance into uncontaminated seawater. The combined data are again amply described by a simple exponential model that can now be used to estimate *p,p'*-DDT levels accrued by planktonic crustacea from seawater containing known concentrations of *p,p'*-DDT.

Materials and Methods

Euphausiids, *Thysanoessa raschii* (M. Sars), were collected year-round in Bedford Basin, Halifax, N.S., with a 1-m diam, 752-μm mesh net towed at about 0.5 m/s. The cod-end of the net was fitted with a 2-L glass container and tows were kept shorter than 10 min to minimize damage to the organisms by water flow. Maximum catches were obtained 2 h after sunset and at a depth of ~10 m. Euphausiids were immediately dipped from the plankton catch with a hand net, stored, and brought back to the laboratory in a plastic cooler. Preliminary culling of sluggish specimens was performed the same evening in a 380-L tank. By the following morning, net-damaged tissues had turned opaque making injured euphausiids conspicuous and easy to cull. Healthy individuals were kept in 10-L glass containers at 5–6°C and fed either *Artemia* nauplii or fresh plankton caught in a 240-μm mesh net.

Seawater spiked with ^{14}C-*p,p'*-DDT (specific activity 5.88 mCi/mM; New England Nuclear Corp.) was prepared as previously described in 2-L glass-stoppered flasks fitted with ground glass discs and Teflon® stopcocks (Harding and Vass 1977). Throughout this study it is assumed that the properties of *p,p'*-DDT in seawater are not affected by adding it in an acetone solution and that it is not appreciably metabolized within the experimental time period (see Darrow and Harding 1975). Euphausiids were held for a day without feeding before ^{14}C *p,p'*-DDT uptake experiments to avoid the possibility of contamination through feeding on their own fecal material (Johannes and Satomi 1966).

In the uptake series of experiments, two euphausiids in 200 mL seawater were transferred to 1.3 L spiked seawater. In all cases seawater was prefiltered twice through GF/C filters which should have removed >99% of particles >2μm (Sheldon 1972). Control flasks contained two euphausiids and carrier volumes of acetone in 1.5 L seawater. Carrier volumes of acetone, <4 μL, had no discernible effect on the viability of the euphausiids. Seawater in experimental and control flasks was changed daily, using stopcocks located at the base, to maintain approximately constant ^{14}C-*p,p'*-DDT concentrations. Four uptake experiments were performed using ^{14}C-*p,p'*-DDT concentrations of 1388 ± 41 (mean ± SE) (July 1975), 1012 ± 56 (July 1975), 455 ± 18 (January 1978), and 27.8 ± 1.5 (August 1975) ng/L. Uptake series were terminated when euphausiids showed erratic behavior and reduced mobility. *p,p'*-DDT was more toxic to euphausiids than to calanoid copepods and caused immobility by the end of the 1st d at 1388 ng/L. If a euphausiid died during an experiment it was removed from the flask the same day so that there was little possibility of cannibalism. Molting rarely occurred during uptake experiments presumably because the euphausiids were not fed.

For clearance studies, euphausiids (three per flask) were placed in ^{14}C-*p,p'*-DDT spiked seawater (2.66 ± 0.04 μg/flask; $n = 6$) for 3 h; then transferred to flow-through seawater (unfiltered) tanks (0.4 m^3) at 4–6°C and removed periodically until the 18th d when the experiment was terminated (see Table 1). The particulate food in the incoming seawater was supplemented weekly with fresh plankton caught in a 240-μm mesh net. It was impossible to record molts under these experimental conditions. ^{14}C-*p,p'*-DDT was below the detection limit, <0.06 ng/mg dry wt, in control euphausiids kept in 505-μm mesh cages of 3725 cm^3 within the same tanks.

Residues of ^{14}C-*p,p'*-DDT and related compounds were extracted from seawater and flasks and prepared for liquid scintillation counting as previously described (Harding and Vass 1977). Initially, euphausiids were extracted as described for copepods (Harding and Vass 1977) to evaluate the *p,p'*-DDT in the lipid compartment. Only 17.2 ± 4.8% ($n = 4$) of the lipid was recovered with this method and so the following simplified method was adopted for euphausiids. Euphausiids were first weighed wet then desiccated under vacuum for 2 d with phosphorus pentoxide. Dry weights obtained in this fashion are equivalent to drying at 60°C to constant weight. Euphausiids were then placed in scintillation vials and crushed into several pieces with stainless steel forceps. Distilled water (0.1 mL) was added, followed by 1.0-mL tissue solubilizer (Soluene 350®, Packard Instrument Co., Inc.). Only the chitinous exoskeleton remained undissolved 25 h later. Permafluor® (15 mL, Packard Instrument Co., Inc.) was added and the sample vial left in the dark for 1 wk which allowed phosphorescence to subside. Samples were counted on a Nuclear Chicago Isocap/300 liquid scintillation counter to give <1.25% SE for each sample.

Results and Discussion

The accumulation of ^{14}C-*p,p'*-DDT from seawater by marine crustaceans could be described by linear equations but this would imply that there is no loss from the organisms. An exponential model was successfully used to interpret the uptake and clearance of *p,p'*-DDT by marine copepods (Harding and Vass 1977), making the assumption that the rates of uptake and clearance are proportional to the *p,p'*-DDT con-

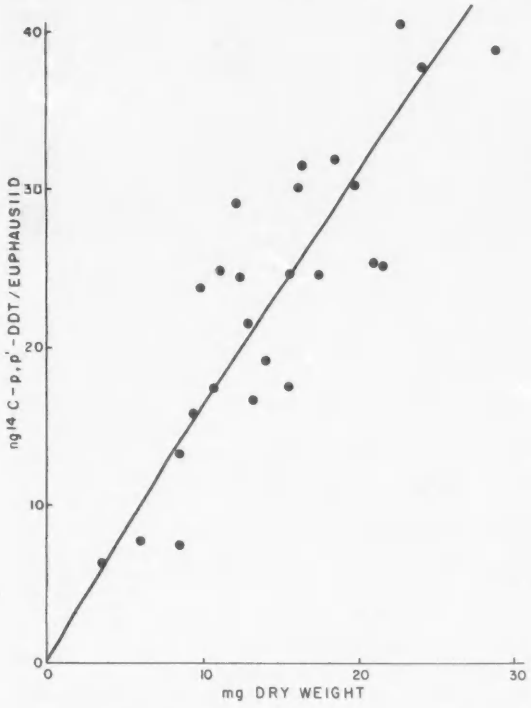

FIG. 1. Relationship between nanograms ^{14}C-p,p'-DDT/euphausiid(E) and body weight (W_d). $E = 1.9\ W_d^{0.93}$ ($r = 0.88$).

centrations in seawater [W] and in or on the organism [C]

$$\frac{d[C]}{dt} = k_i \frac{\mu}{\alpha}[W] - k_j[C] \tag{1}$$

where k_i and k_j are the rate constants onto or into, and out of the organisms, respectively, and μ/α was intended as a surface area term (see Ruzic 1972).

To quantify the surface area term, a method was developed but at present cannot be used for organisms smaller than euphausiids (Harding 1977). The surface area, S (in mm^2), of *Thysanoessa raschii* was found to be proportional to dry weight, W_d (in mg),

$$S = 31.1\ W_d^{0.95\pm0.06}\ (r = 0.97)$$

with the 95% confidence intervals given. This near proportionality of surface area to dry weight is likely due to the importance of the exoskeleton in terms of dry weight. Euphausiids of various sizes were placed in seawater spiked with 2.54 ± 0.14 μg ^{14}C-p,p'-DDT/flask as described above. The concentration of ^{14}C-p,p'-DDT on or in each euphausiid (E: ng/euphausiid), after 3-h exposure, is plotted against dry weight in Fig. 1. A power function best describes the data,

$$E = 1.9\ W_d^{0.93\pm0.19}\ (r = 0.88)$$

where W_d is again the dry weight (mg) of the euphausiid. The similarity of exponents between this and the previous equation suggests that the concentration of p,p'-DDT taken up by euphausiids is proportional to the surface area exposed. It follows that the effect of different surfaces exposed should be removed by expressing the concentration of p,p'-DDT in and on the organism per unit dry weight, E/W_d or [C].

The general equation (1) should accordingly be simplified as follows:

$$\frac{d[C]}{dt} = k_i[W] - k_j[C] \tag{2}$$

or in the integrated form

$$[C] = \frac{k_i}{k_j}[W](1 - e^{-k_j t}). \tag{3}$$

For the clearance experiment where [W] approaches zero, equation (2) becomes

$$\frac{d[C]}{dt} = -k_j[C]. \tag{4}$$

Integrating this equation with a given initial [C] at time $t = 0$, [C_0], we have

$$[C] = [C_0]\ e^{-k_j t}. \tag{5}$$

The clearance of p,p'-DDT by euphausiids shown in Table 1 and Fig. 2 is best fitted to a negative exponential equation through standard regression analy-

TABLE 1. Clearance of ^{14}C-p,p'-DDT by *Thysanoessa raschii* in flowing seawater. *Mean ± SE.

Time (d)	Euphausiid dry weight (mg)	^{14}C-p,p'-DDT concn in/on euphausiid		Number euphausiids analyzed
		ng/mg dry wt	ng/mg wet wt	
0	19.12±2.19*	2.07±0.25	0.62±0.10	9
1	12.96±1.54	1.87±0.17	0.48±0.06	5
3	14.38±1.49	1.65±0.20	0.42±0.06	5
4	17.90±1.51	1.55±0.24	0.41±0.06	5
5	18.27±4.89	1.54±0.50	0.39±0.08	2
10	15.92±1.98	1.06±0.20	0.25±0.05	5
18	14.97±1.02	0.95±0.21	0.22±0.05	5

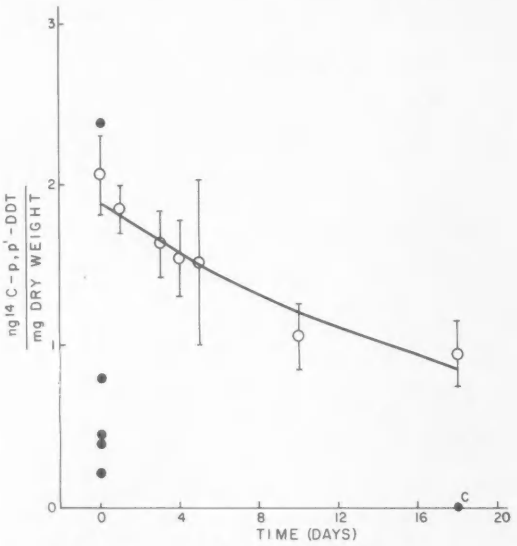

FIG. 2. Clearance of ^{14}C-*p,p'*-DDT from *Thysanoessa raschii* in flowing seawater tanks: ○ active, and ● sickly individuals. C denotes controls.

sis on ln-transformed data

$$[C] = \frac{E}{W_d} = 1.90\, e^{-0.043t} \quad (r = 0.92).$$

The clearance rate constant k_j does not differ significantly ($0.5 < P < 0.6$) from that previously reported for copepods, $k_j = 0.048$ (Harding and Vass 1977). It is suspected that the external surface of an organism is also an important factor in determining the clearance rate of *p,p'*-DDT from the presence of the W_d term.

Five euphausiids that were either sickly or had died during the initial uptake of *p,p'*-DDT are also plotted in Fig. 2. Four of these euphausiids contain considerably less *p,p'*-DDT than their apparently healthy counterparts. This suggests that the activity or health of an organism affects the uptake process. This conclusion is supported by the results of Crosby and Tucker (1971) who found that heat-killed *Daphnia* accumulated half as much DDT as healthy individuals, and by those of Wildish and Zitko (1971) who found that heat-killed *Gammarus* did not take up measurable quantities of polychlorinated biphenyls. Murphy and Murphy (1971) reported that dead mosquito fish (*Gambusia*) accumulated 0.3 ng DDT/fish compared with 9.6 ng/live fish from 20°C water over 2 d. Several studies with fish have all demonstrated that more DDT is taken up from water at higher temperatures (Murphy and Murphy 1971; Reinert et al. 1974; see Kenaga 1975). However, Cox (1971b) and Wilkes and Weiss (1971) found little difference in DDT uptake between live and heat-killed euphausiids and unfrozen dragonfly nymphs, respectively. Now, it is generally accepted that organochlorines are initially adsorbed or absorbed to the body and respiratory surfaces then absorbed into the organism via the circulatory system (Addison 1976). The simplest explanation of the fact that dead or sickly euphausiids take up less *p,p'*-DDT is that the surface area in contact with the pesticide is less per unit time and that this is ultimately controlled by the metabolic activity of the organisms.

Setting k_j equal to 0.048/d, uptake data (Table 2) can be fitted to equation (3) by the process of iteration

TABLE 2. Uptake of ^{14}C-*p,p'*-DDT by *Thysanoessa raschii* from seawater of 27.8, 455, 1012, and 1388 ng/L. *Mean ± SE.

DDT in seawater (ng/L)	Time	Euphausiid dry weight (mg)	DDT concn in/on euphausiid		DDT concentration associated with		Number euphausiids analyzed
			ng/mg dry wt	ng/mg wet wt	Container walls (ng)	Seawater (ng/L)	
27.8±1.5	1 d	16.80±1.17*	0.32±0.04	0.06±0.01	9.8±1.3	21.5±0.8	4
	2 d	17.70±1.01	0.64±0.01	0.19±0.03	12.5±0.2	26.5±0.1	4
	4 d	28.16±1.01	1.06±0.10	0.23±0.01	14.0±1.3	29.2±0.3	4
	10 d	14.40±2.65	2.38±0.32	0.39±0.05	16.1±2.5	27.1±0.3	3
	14 d	16.27±0.98	3.46±0.13	0.59±0.09	14.2±5.6	34.5±2.8	4
455±18	1 d	14.85±0.71	3.96±1.36	1.02±0.34	181.3±116.0	461±38	4
	2 d	16.21±1.54	9.41±1.60	2.35±0.47	208.5±82.2	412±18	5
	3 d	16.10±1.59	9.44±1.73	1.87±0.23	305.4±4.4	449±18	3
	4 d	17.12±1.42	11.88±1.35	3.49±0.37	497.0±142.7	434±50	3
	6 d	14.16±1.17	19.52±1.36	4.26±0.42	388.1±76.3	543±37	5
1012±56	12 h	33.30±3.39	5.36±0.41	1.13±0.08	596.7±172.2	905±148	4
	24 h	33.71±2.12	7.99±0.86	1.61±0.20	652.9±36.7	1055±78	4
	48 h	22.40±3.52	18.54±1.92	3.53±0.68	709.9±174.8	1075±48	4
1388±41	4 h	30.20±3.17	3.11±0.33	0.65±0.06	489.3±77.6	1460±6	4
	6 h	26.39±3.29	4.62±0.55	1.07±0.09	485.1±19.5	1316±7	4

TABLE 3. Values of ^{14}C-*p,p'*-DDT concentration in seawater, flux rates of ^{14}C-*p,p'*-DDT in/on copepods[a] and euphausiids, and predictive equations using $k_j = 0.048$.

$W \pm$ SE; N ng/L	Organism	$k_1 \times 10^{-4}$/d	$(k_1/k_j) \times 10^{-5}$	Fitted equations; r
27.8±1.5; 10	*Thysanoessa*	1.19	2.48	$C = 6.9\,[1 - e^{-(0.048/d)t}]$; 0.97
32.5±0.7; 6	*Calanus*, adults	1.04	2.18	$C = 7.1\,[1 - e^{-(0.048/d)t}]$; 0.96
36.3±2.3; 8	*Calanus*, IV and V	2.51	5.23	$C = 19\,[1 - e^{-(0.048/d)t}]$; 0.98
324±13; 8	*Calanus*, adults	1.73	3.61	$C = 117\,[1 - e^{-(0.048/d)t}]$; 0.98
355±8; 15	*Calanus*, IV and V	1.83	3.83	$C = 136\,[1 - e^{-(0.048/d)t}]$; 0.99
455±18; 11	*Thysanoessa*	0.76	1.58	$C = 72\,[1 - e^{-(0.048/d)t}]$; 0.88
1012±56; 6	*Thysanoessa*	0.93	1.93	$C = 196\,[1 - e^{-(0.048/d)t}]$; 0.93
1388±41; 4	*Thysanoessa*	1.21	2.52	$C = 350\,[1 - e^{-(0.048/d)t}]$; 0.70
1337±30; 8	*Calanus*, adults	1.26	2.61	$C = 350\,[1 - e^{-(0.048/d)t}]$; 0.97

[a]In our earlier publication (Harding and Vass 1977) the k_t values were incorrectly written as $y \times 10^3$/d instead of $y \times 10^9$/d both in the text and Table 4.

after logarithmic transformation,

$$\ln\left(\frac{K[W]}{K[W] - [C]}\right) = k_j t$$

where $K = k_i/k_j$. Our results give us confidence in the use of the model equation (3) and are summarized in Table 3, together with the results from copepod experiments taken from Harding and Vass (1977). The rate constants derived from experiments using concentrations of *p,p'*-DDT ranging from the maximum solubility in water (Biggar and Riggs 1974) to nanograms per litre levels are very similar. Furthermore, there appears to be no trend in k_i values over the range of *p,p'*-DDT concentrations used. This indirectly supports our belief that the experiments involving higher concentrations of *p,p'*-DDT (1.3 μg/L) were terminated before toxic effects drastically affected the mobility of the organisms (see Materials and Methods). Grosch (1967) found 100% mortality of *Artemia salina* populations after 5-d exposure in 100 ng/L DDT brine solution and 39% mortality after 21 d at 1 ng/L. However, the *Artemia* were fed yeast in the contaminated brine which would have increased their uptake of DDT by consumption of sorbed DDT on and in the yeast cells.

The close correspondence between euphausiid and copepod uptake rate constants support our contention that the possible effect of different surface area exposed is reduced by expressing the concentration of *p,p'*-DDT in or on an organism on a dry weight basis. Implicit in this reasoning is the assumption that a similar relationship between surface area and dry weight applies to both *Calanus* and *Thysanoessa*. We now consider whether surface area per unit time is a more important factor in the uptake process than just surface area. Mature *Thysanoessa* weighing 20 mg have a surface area of ~200 mm² by geometric approximation to a right circular cylinder, or ~10 mm²/mg. Similarly, a 0.65-mg adult *Calanus* has a surface area of ~22 m², or ~34 mm²/mg. Now, a moving organism exposes itself to a continuously renewed supply of DDT since the insecticide is adsorbed on contact. Hardy and Bainbridge (1954) experimentally measured the swimming speeds of both *Calanus* and euphausiids and report rates of 15–47 m/h and 40–128 m/h, respectively. More recent estimates from field data on vertically migrating populations are 36–108 m/h for *Calanus finmarchicus* and 180–216 m/h for euphausiids (Klyashtorin and Yarzhombek 1973). Both studies, however, suggest that euphausiids swim about 2.7 times as fast as *Calanus* (calculated from median values) which indicates that the surface area exposed per milligram per unit time should be about equal. This very simply explains why the experimentally derived k_i's for *Thysanoessa* and *Calanus* are so similar.

For whatever reason, equation (3) adequately describes the *p,p'*-DDT dynamics of two different sizes of zooplankters in seawater. It is instructive to test equation (3) for general applicability to a marine crustacean zooplankter assuming the metabolites of *p,p'*-DDT behave in a similar manner to *p,p'*-DDT. A boreal copepod, starting as a first nauplius, has a life span of 1–2 mo or 8 mo depending on whether it overwinters in late copepodid stages (Corkett and McLaren 1978; Marshall and Orr 1955). Boreal euphausiids have life expectancies of 2–3 yr (Mauchline and Fisher 1969). There is sufficient time for an equilibrium to be established in organisms with a life span of >2 mo, so that $[C] = (k_i[W]/k_j)$. Levels of ΣDDT (i.e. *p,p'*-DDT and metabolites) in the world oceans range from <0.01 to 6.1 ng/L (see Dawson and Riley 1977; Osterroht 1977; Stadler 1977). Greater contamination has been reported in polluted coastal regions such as San Francisco Bay (2–23 ng/L; Earnest and Benville 1971) and in the Mediterranean near Marseille (80–180 ng/L; Raybaud 1972, quoted by Dawson and Riley 1977) and in surface slicks (38 mg/L, Larsson et al. 1974; 4.4–14.6 ng/L, Stadler and Ziebarth 1976). It is well known that ΣDDT adsorbs on to surfaces of suspended particles (Biggar and Riggs 1974; Cox 1971a) and is then absorbed into living particles (Södergren 1968). Reported values of ΣDDT in seawater, however, include this ΣDDT which is bound to particles, organic and in-

TABLE 4. Records of ΣDDT levels in marine pelagic and planktonic crustacea.

Author(s)	Organism	Location, year, type	ppb (ng/g) Wet wt	Dry wt	Lipid wt	n[b]
Baird et al. 1975	bulk plankton[a] >333 μm	Gulf of Mexico, 1973, oceanic	2–3[f]		205–3681	5
Claeys et al. 1975	*Pandalus jordani*[b]	Off Oregon, USA, 1971, coastal	1.1–5.0			13
	sand shrimp		<0.3–2.0			3
	Euphausia pacifica[c]		0.2–5.9			14
Cox 1971b	*Euphausia pacifica*[c]	Off California, USA, 1970, coastal	~100–450	~500–2500		5
	copepods		250			1
Darrow and Harding 1975	*Calanus* sp.[d]	Off St. Marg. Bay, N.S., coastal	<1			1
Giam et al. 1973a	decapod larvae[b]	Ross Sea, Antarctic, 1971–72, oceanic	<0.3			1
	bulk plankton		<0.8			1
	Euphausia crystallorophias[c]		<0.4			1
Giam et al. 1973b	bulk plankton >230 μm	Gulf of Mexico, 1971–72, oceanic	<0.2–34			29
Harvey et al. 1972	bulk plankton >239 μm	N Atlantic, 1970–71, oceanic	<0.01–9.5			4
	Systellaspis debilis[e]		3.1–5.7		168–169	2
Harvey et al. 1974	*Pandalus borealis*[b]	Denmark Str., Iceland, 1971, oceanic	1		27	1
		Georges Bank, USA, 1971, coastal	7		500	1
	Acanthephyra sp.[e]	N and S Atlantic, 1971–72, oceanic	3–17		37–890	3
	Systellaspis debilis[e]	1970–72	3–12		100–1700	6
Risebrough et al. 1972	bulk plankton >239 μm	NW Atlantic Shelf, 1969, 71, coastal		2.5–16(110)[g]	42–7000	14
		N Atlantic, 1970, oceanic	<0.01			2
		S Atlantic, 1971, oceanic	0.2–2.6		91–500	4
Sameoto et al. 1975	*Thysanoessa raschii*[c]	Gulf of St. Lawrence, N.S., 1973–74, coastal	8.7–22		491–1457	4
	Thysanoessa inermis[c]		8.5–12.4		92–1121	6
	Meganyctiphanes norvegica[c]		25.1–64.8		918–2655	12
Ten Berge and Hillebrand 1974	bulk plankton >300 μm	North Sea off Holland, 1973, coastal	1.3		560	2
	shrimp[b]		2.9		260	2
Williams and Holden 1973	bulk plankton >300 μm	Firth of Clyde, Scotland, 1971–72, coastal	25–107			12
		Atlantic off Scotland, 1971–72, oceanic	2–16(50)			13
Woodwell et al. 1967	bulk plankton >239 μm	Long Is., N.Y., USA, 1966, estuarine	40			1

[a]Marine zooplankton is usually more than 90% crustacean; [b]decapod shrimp; [c]euphausiid shrimp, krill; [d]copepod; [e]mesopelagic decapod shrimp; [f]range; [g]abnormally high value in brackets; [h]number of samples analyzed.

organic. We have found that up to 50% of the organochlorines present in seawater off Nova Scotia are associated with particles that are removed by a 0.22-μm filter. However, the possibility that "dissolved" organochlorines are adsorbing to the filter surface cannot be excluded. All of our experiments were performed with GF/C filtered (2×) seawater to exclude the possibility of uptake through feeding. If we use 0.1 ng/L ΣDDT in seawater and $k_i = 1.2 \times 10^4$/d, a summer *Calanus* with a life span of 20 d would accumulate 15.4 ng/g dry wt ΣDDT or ~5.5 ng/g wet wt from seawater. The same calculation with larger organisms with >2½-mo life spans, such as *Thysanoessa* and overwintering *Calanus* leads to estimates of ~9 ng/g wet wt ΣDDT. At such low levels of ΣDDT in seawater it becomes necessary to correct these estimates by adding the "naturally" occurring DDT in our laboratory animals (Darrow and Harding 1975; Sameoto et al. 1975). Revised estimates are ~6.5 ng/g for *Calanus* and 19 ng/g wet wt for *Thysanoessa*. These values fall well within the range of observed ΣDDT concentrations in crustacean zooplankters (literature summary in Table 4). Also apparent from this collation is the lack of evidence for greater concentrations in larger crustaceans such as shrimp and euphausiids. An additional source of ΣDDT that we have ignored up to now is that available through feeding. Cox (1971b) has shown that *Euphausia pacifica* retains 60–80% of the ΣDDT ingested in or on food items after 2 d. This indicates that our choice of 0.1 ng/L ΣDDT in seawater is an overestimate and that appreciably more of the ΣDDT reported in seawater must be "bound" to particles.

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A Reason for Pleomerism

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SPOUGE, J. L., AND P. A. LARKIN. 1979. A reason for pleomerism. J. Fish. Res. Board Can. 36: 255–269.

Pleomerism, the increase in vertebral number with maximum recorded length for species within a family, may be explained for fish by hydrodynamic considerations. A model is developed that suggests that the upper limits of the slope of the relation between log vertebral number and log length should be 0.43 in laminar flow and 0.35 in turbulent flow. These slopes are compared with those of previous studies only with difficulty because (1) those values were for predictive rather than functional regressions, (2) the slope will depend on the range in length of various species across temperature zones, and (3) no distinction was made between structural and locomotor vertebrae. Variations in shape also complicate the relation between vertebral count and length, there are latitudinal factors involved, and maximum length is probably only a weak correlate of the length at which natural selection may be concentrated. When these factors are considered, it is to be expected that observations would provide only a rough approximation to theory.

The theory underlying the model is also used to derive a formula for the stride length of fish motion that is then compared with empirical results.

Key words: vertebrae counts, body size, locomotion, hydrodynamic equations, mathematical model, stride length

SPOUGE, J. L., AND P. A. LARKIN. 1979. A reason for pleomerism. J. Fish. Res. Board Can. 36: 255–269.

Des considérations hydrodynamiques peuvent expliquer le pléomérisme, soit l'augmentation du nombre de vertèbres en fonction de la longueur maximale enregistrée pour l'espèce au sein d'une famille. Nous construisons un modèle qui donne à penser que les limites supérieures de la pente de la relation log du nombre vertébral-log de la longueur devrait être 0,43 dans un écoulement laminaire et 0,35 dans un écoulement turbulent. Ces pentes se comparent difficilement avec celles d'études antérieures parce que (1) ces valeurs s'appliquent à des régressions prévisionnelles plutôt que fonctionnelles, (2) la pente dépend de la gamme des longueurs observées chez diverses espèces à travers des zones de températures et (3) on ne distingue pas entre vertèbres structurales et vertèbres locomotrices. La relation entre le nombre vertébral et la longueur se complique de plus du fait que la forme varie, que des facteurs latitudinaux entrent en jeu et que la longueur maximale n'est probablement qu'un faible corrélatif de la longueur à laquelle la sélection naturelle se concentre. Compte tenu de ces facteurs, on doit s'attendre que les observations ne donnent q'une approximation grossière de la théorie.

On se sert aussi de la théorie sur laquelle est fondé le modèle pour déduire une formule donnant la longueur de lancée du poisson que l'on compare ensuite aux résultats empiriques.

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LINDSEY (1975) assembled a large body of evidence that showed that for many families of fish there is a positive correlation between vertebral number (V) and maximum recorded length (L) for species within a family, and that this relationship is approximated by $V = CL^m$ (i.e. log V vs. log L is approximately linear). This phenomenon he termed "pleomerism." (All units used are centimetre-gram-second.)

Lindsey also observed that Jordan's Rule (cold-water fish have more vertebrae than related warmwater fish) is reinforced by pleomerism because there is a coupling of temperature gradients with gradients in maximum recorded length. Nevertheless, Jordan's Rule still holds if similar fish of the same length are compared for vertebral number across different temperature zones.

The intention of this paper is to show that both pleomerism and Jordan's Rule might be consequences of the laws of hydrodynamics as they apply to fish of similar structure but different dimensions, swimming in the anguilliform or carangiform modes of motion. (A survey of fish motion is given in Webb 1975).

LIST OF SYMBOLS

Unless otherwise indicated

Bars over variables denote time-averages.

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Subscripts lam and turb indicate variables for laminar and turbulent flow respectively.
Subscript o indicates a maximum value (which may quite often be at the tail).
Lower case English letters denote relative dimensions.
Singly primed lower case English letters denote relative dimensions of the spinal musculature.

English Letters

a'	relative cross-sectional area of spinal musculature averaged over length of locomotor spine
A	surface area of fish
b''	see Fig. 3
c	ratio of lengths, caudalmost vertebra to "average" vertebra
c_f	coefficient of frictional drag
c_{tot}	coefficient of total drag
C	Lindsey's value of V for $L = 1$
dx	length of caudalmost vertebra
$h(x, t)$	lateral displacement of fish. See Fig. 1
L	Lindsey's maximum recorded length for a species, or length of the hypothetical fish
m	Lindsey's exponent relating V and L or virtual mass of the water pushed by a fish per unit length
M	momentum imparted to the water per unit fish length
O, O'	see Fig. 3
P	mechanical power output per weight muscle at velocity U
Q, Q'	see Fig. 3
R	Reynold's Number
S	cross-sectional depth of fish either for arbitrary section in equation (10) or averaged along the fish's length
t	time
T	Wardle's twitch time or ½ period of caudal motion
$\bar{T}$	time-averaged wasted kinetic energy per length of fish
U	maximum fish speed, either burst or sustained
U_F	Lighthill's V, the speed of the propulsive wave along the fish's length
v	proportion of fish length occupied by locomotor vertebrae
V	Lindsey's mean vertebral count for a species or number of locomotor vertebrae in a fish
V_o	number of structural vertebrae
w	$\partial h/\partial t + U\,\partial h/\partial x$ = lateral speed of a passing water particle
W	$\partial h/\partial t$ = lateral velocity of a segment of a fish
x	distance from anterior tip of the fish
Y	a sinusoidal function (Appendix A)
Z	axis of lateral fish motion, see Fig. 1

Greek Letters

β	virtual mass coefficient, see equation (10)
η	hydromechanical efficiency
κ	parameter describing depth and lateral velocity of passing water particles along the length of the fish
λ	absolute wavelength of fish propulsive wave near tail
μ	viscosity of water
ρ	density of water
Σ	maximum velocity of contraction per unit length of caudalmost vertebral musculature at velocity U
τ	parameter like κ
τ_o	½ period of sinusoidal function Y (Appendix A)
ω	angular velocity of tail motion function and Y

Lighthill's Models

The relevant portions of models for anguilliform and carangiform motions from Lighthill (1970) will be outlined here. Lighthill developed these models for purposes other than ours, so the assumption that these models are valid for the purposes of this paper has to be made explicitly. (For discussion of Lighthill's assumptions in deriving the models reference should be made to the source.) The purpose of this section is to present some of Lighthill's equations and to manipulate them mathematically into suitable forms. In particular Lighthill's formulae for thrusts produced by anguilliform and carangiform motion will be shown to be equivalent *for the purposes of this paper*.

Due to necessary inconsistencies between symbols in Lighthill's paper and this paper, the equations from that paper may appear here in a different symbolism. Wherever Lighthill's equations are introduced, their numbers in his paper are indicated by numbers in italics. after the equation numbers of this paper.

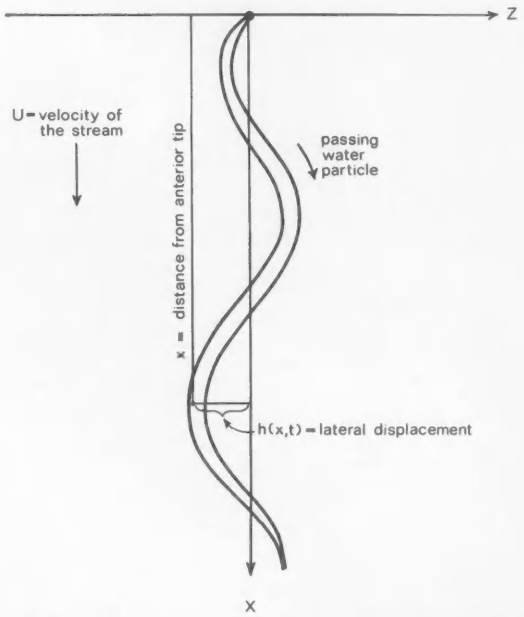


FIG. 1. Diagrammatic representation of dorsal perspective of anguilliform swimming motion. See text for definition of symbols.

ANGUILLIFORM MOTION

Figure 1 depicts an anguilliform fish moving in a stream of velocity u so that the fish makes no progress. The following definitions are relevant (see Fig. 1):

$h(x, t)$ = lateral displacement of the fish at a distance x from the anterior tip at time t

$W(x, t) = \dfrac{\partial h}{\partial t}$ = lateral velocity of the fish

$w(x, t) = \dfrac{\partial h}{\partial t} + U\dfrac{\partial h}{\partial x}$ = lateral velocity of passing water

= lateral velocity of fish + lateral velocity of passing water if the fish were unmoving in its position at time t.

m = virtual mass of water pushed by the fish per unit length.
(The fish pushes the water laterally at velocity w and gains momentum mw per unit length. This defines m, the virtual mass per unit length.)

From Lighthill (1970),

(1) (*11*) instantaneous thrust

$$= [mw(W - \tfrac{1}{2}w)]_{x=L} - \frac{\partial}{\partial t}\int_o^L \left(mw\frac{dh}{dx}\right)dx.$$

The subscript $x = L$ indicates that values are to be taken at the tail of the fish. The latter term is the change in time of a fluctuating quantity and has a net change of zero if time-averaged (bars over variables indicate time averages). Hence,

(2) time-averaged thrust $= \overline{[mw(W - \frac{1}{2}w)]}_{x=L}$

$$= [m(\overline{wW} - \tfrac{1}{2}\overline{w^2})]_{x=L}$$

$$= m\{[\overline{wW}]_{x=L} - \tfrac{1}{2}[\overline{w^2}]_{x=L}\}$$

(m is constant in time and is therefore its own time-average.) Near the tail (for $x = L$) Lighthill states

(3) (*3*) $$w = \frac{U_f - U}{U_f}W$$

where U_f is Lighthill's V (in this paper, V is reserved for number of vertebrae) and is the velocity of the wave motion that is generated by the fish and travels backwards along the fish's length.

From (3) the following are derived:

(4) $[w^2]_{x=L} = \left(\dfrac{U_F - U}{U_F}\right)^2 [W^2]_{x=L}$ by squaring

(5) $[wW]_{x=L} = \left(\dfrac{U_F - U}{U_F}\right) [W^2]_{x=L}$ by multiplying by w.

Because $(U_F - U)/U_F$ is a constant over time, time-averaging the two equations and then dividing (4) by (5) yields

(6) $$\frac{[\overline{w^2}]_{x=L}}{[\overline{wW}]_{x=L}} = \frac{U_F - U}{U_F}.$$

But Lighthill gives

(7) (*12*) $$\eta = 1 - \tfrac{1}{2}\frac{[\overline{w^2}]_{x=L}}{[\overline{wW}]_{x=L}}$$

where η is the hydromechanical efficiency of motion, given by

$$\eta = \frac{\text{mechanical power required}}{\text{mechanical power expended}}.$$

Combining (6) and (7) and solving for $(U_F - U)/U_F$ gives

(8) $$\frac{U_F - U}{U_F} = 2(1 - \eta).$$

Substituting (8) into (4) and (5) and time-averaging both resulting equations produces

$$[\overline{w^2}]_{x=L} = 4(1 - \eta)^2[\overline{W^2}]_{x=L}$$

$$[\overline{wW}]_{x=L} = 2(1 - \eta)\,[\overline{W^2}]_{x=L}.$$

Substituting these back into equation (2) yields

(9) time-averaged thrust

$$= m(2(1 - \eta)[\overline{W^2}]_{x=L} - 2(1 - \eta)^2[\overline{W^2}]_{x=L})$$

$$= m \cdot 2[\overline{W^2}]_{x=L} \cdot \eta(1 - \eta)$$

$$\cong \frac{\pi}{4} S_o^2 \cdot 2[\overline{W^2}]_{x=L} \cdot \eta(1 - \eta).$$

The last approximation arises from

(10) (*4*) $$m = \frac{\pi}{4}\beta\rho S^2.$$

Where β is a virtual mass coefficient, a dimensionless number dependent only on cross-sectional shape, S is the depth of the fish's cross section and, ρ is the density of the surrounding water. For many cross sections $\beta \cong 1$ (Lighthill 1970) and $\rho \cong 1$, and in consequence,

(11) $$m \cong \frac{\pi}{4} S_o^2 \quad \text{at the tail}$$

where S_o is the depth of the cross section at the tail (see Fig. 2).

If the lateral speed $[W]_{x=L}$ of the anguilliform fish's tail is approximately harmonic with time (i.e. it produces a near-sine wave when graphed against time), and if W_o is the maximum lateral velocity of the tail, by a standard formula (see Appendix A):

$$[\overline{W^2}]_{x=L} = \frac{W_o^2}{2}.$$

Substituting for $[\overline{W^2}]_{x=L}$ in equation (9) gives

(12) time-averaged thrust $\cong \dfrac{\pi}{4} S_o^2 W_o^2 \eta(1 - \eta)$.

This equation is the crucial one of this section. The scaling of the parameter W_o will be shown to involve vertebral number and will be the crux of relating the scaling of vertebral number with length.

For those interested in the derivation of the model, reference may be made to Lighthill (1970); otherwise the content of equation (12) is sufficient: the thrust a fish generates is proportional to the squares of both its depth and tail velocity and has a dependency on the hydromechanical efficiency of the fish. The next section demonstrates that equation (12) is approximately true for carangiform motion as well as anguilliform motion.

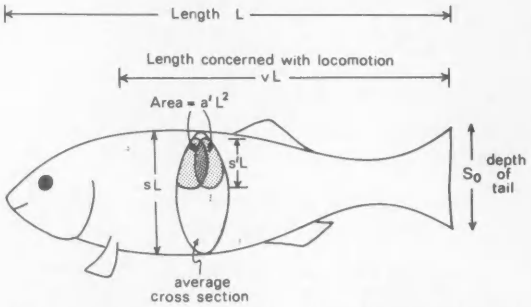


FIG. 2. Illustrating symbols for dimensions of a fish and its vertebral musculature. See text for definition of symbols.

CARANGIFORM MOTION

Under a similar frame of reference (Fig. 1) Lighthill gives a model for carangiform motion. Defining momentum imparted to the water as M and the time-averaged kinetic energy wasted as $\overline{T}$, both per unit fish length, Lighthill derives

(13) (*31*) time-averaged thrust $= \left[\left(\frac{U_F}{U_F - U}\right)\overline{Mw} - \overline{T}\right]_{x=L}$

(14) (*32*) $\eta = 1 - \left(\frac{U_F - U}{U_F}\right)\frac{[\overline{T}]_{x=L}}{[\overline{Mw}]_{x=L}}.$

These equations differ in form from those for anguilliforms because the tails of carangiforms are more specialized, being much deeper and exerting a more powerful lateral thrust than the rest of the body. These natural facts are reflected by the parameters $\tau - \kappa$ and $2\kappa - \tau$ in the equations

$$w(x, t) = w_o e^{(\tau-\kappa)(x-L)} \cos \omega(t + (L - x)U_F^{-1})$$
$$S(x) = S_o e^{(2\kappa-\tau)(x-L)}$$

which are derived from Lighthill's (*34*) and (*38*). The first is (*38*) divided by (*34*); the second (*38*) divided by the square of (*34*), S_o is the depth at the tail of the fish (see Fig. 2), w_o is the maximum lateral velocity of a passing water particle at the tail (since the maximum occurs when the cos = 1, and "at the tail" is when $x = L$).

The factors $e^{(\tau-\kappa)(x-L)}$ and $e^{(2\kappa-\tau)(x-L)}$ represent "growth" of their respective variables, $w(x, t)$ and $S(x)$, toward the tail. To ensure growth (and not reduction) $\tau - \kappa$ and $2\kappa - \tau$ must both be positive, yielding $\kappa \leq \tau \leq 2\kappa$. For anguilliforms the growth of the variables, depth and lateral water velocity, is small, so κ is small (thereby making τ small). For carangiform motion κ is large.

Lighthill (1970) also gives

(*36*) $[\overline{Mw}]_{x=L} = \frac{3}{8}S_o^2 w_o^2 + \frac{\frac{3}{8}\rho S_o w_o^3 \kappa}{U[\kappa^2 + \omega^2(U^{-1} - U_F^{-1})^2]}$

(*38*) $[\overline{T}]_{x=L} = \frac{3}{16}\rho S_o^2 w_o^2 + \frac{3}{8}\rho S_o w_o^3 U^{-1}\tau^{-1}.$

After algebraic manipulation and setting $\rho \cong 1$

(15) $[\overline{Mw}]_{x=L} = \frac{3}{8}S_o^2 w_o^2\left(1 + \frac{1}{2}\frac{\kappa S_o^{-1}}{[\kappa^2 + \omega^2(U^{-1} - U_F^{-1})^2]} \cdot \frac{2w_o}{U}\right)$

(16) $[\overline{T}]_{x=L} = \frac{3}{16}S_o^2 w_o^2\left(1 + \frac{S_o^{-1}}{\tau} \cdot \frac{2w_o}{U}\right).$

Lighthill states that

(a) $\frac{2w_o}{U}$ is of the order of 1 for many fish

(*b*) τ, κ are "significantly larger" than S_o^{-1} for carangiform motion.

Stated formally,

(17) $$\frac{2w_o}{U} \cong 1$$

(18) $$\frac{S_o^{-1}}{\tau} \cong \frac{S_o^{-1}}{\kappa} \cong 0$$

If the second terms in each bracket of equations (15) and (16) are examined

$$\tfrac{1}{2}\frac{\kappa S_o^{-1}}{[\kappa^2 + \omega^2(U^{-1} - U_F^{-1})^2]} \cdot \frac{2w_o}{U} \cong \tfrac{1}{2}\frac{\kappa S_o^{-1}}{[\kappa^2 + \omega^2(U^{-1} - U_F^{-1})^2]}$$
$$\leq \tfrac{1}{2}\frac{\kappa S_o^{-1}}{\kappa^2} = \tfrac{1}{2}\frac{S_o^{-1}}{\kappa}$$
$$\cong 0$$
$$\frac{S_o^{-1}}{\tau} \cdot \frac{2w_o}{U} \cong \frac{S_o^{-1}}{\tau} \cong 0.$$

Substituting these approximations back into equations (15) and (16) yields

(17) $$[\overline{Mw}]_{x=L} \cong \tfrac{3}{8}S_o^2 w_o^2$$

(18) $$[\overline{T}]_{x=L} \cong \tfrac{3}{16}S_o^2 w_o^2.$$

If (17) and (18) are substituted into (14) there results

$$\eta = 1 - \tfrac{1}{2}\left(\frac{U_F - U}{U_F}\right)$$

so that equation (8) is again derived.

Substituting (17), (18), and (8) into (13) yields

(19) time-averaged thrust $= \tfrac{3}{4}S_o^2 \cdot \frac{w_o^2}{4} \cdot \frac{\eta}{1 - \eta}.$

Lighthill states that equation (3) holds for carangiform swimmers as well as anguilliforms. Since equation (8) still holds as well, $w = 2(1 - \eta)W$ at the tail. Since the above holds for the maximal values of both sides at the tail (i.e. when $w = w_o$ and $W = W_o$), substitution of the above equation into equation (19) gives

(20) time-averaged thrust $= \tfrac{3}{4}S_o^2 W_o^2 \eta(1 - \eta)$

which is equation (12) if one accepts $\pi \cong 3$. Accordingly from this point onward, (20) will be considered representative of the pair of equations (12) and (20).

One of the points of Lighthill's paper was that carangiforms are more efficient than anguilliforms. In

the course of applying approximations (17) and (18), η appears to be the same for carangiforms as anguilliforms. This apparent contradiction is readily explained. The advantage of a small increase in hydromechanical efficiency may well have been enough to lead to the evolution of the carangid form, but for the scaling of vertebral numbers, this increase is irrelevant. This makes sense: one would not expect a small change in hydromechanical efficiency per se to significantly affect the vertebral count. Increased efficiency, though significant to survival, is not equally significant to vertebral morphology.

A Model for Pleomerism

The aim of this section is to develop a formula illustrating the dependence of the vertebral number (V) of a fish on its other physical parameters, one of which is its length (L). Towards this end, in a manner parallel to that of Bainbridge (1961), power produced will be equated to power required to yield an expression for the maximum speed (U) of the fish. Then thrust produced will be shown to have a dependence on the vertebral number (V). Finally the equivalence of thrust (involving V) and drag (involving U) yields an equation from which U may be eliminated. The resultant expression can then be solved for V.

In the following, "maximal speed" is taken to mean that speed, either burst or sustained, at which selection acts most vigorously.

Derivation of U

A *locomotor vertebra* is defined as a vertebra actively involved in propulsion of the fish. Other vertebrae are called *structural vertebrae*. Let the proportion of the fish's length occupied by locomotor vertebrae be v (Fig. 2). (Lower case English letters in this section are relative measures and therefore dimensionless unless stated otherwise.) Then:

(21) total length of locomotor vertebrae $= vL$.

Three variables define locomotor musculature cross section and are primed to so indicate. They are ratios between dimensions of this cross section and appropriate powers of the length of the fish and are dimensionless:

$$a' = \frac{\text{average area of locomotor musculature}}{L^2}$$

$$s' = \frac{\text{average depth of locomotor musculature}}{L}$$

where the averages are taken along the length of the locomotor musculature.

We now define b', a measure of the relative breadth of the locomotor musculature, by

$$b' = \frac{a'}{s'} = \frac{\text{average area}}{\text{average depth}} \cdot \frac{1}{L}.$$

From the above definitions we derive

(22) Average cross section of locomotor musculature $= a'L^2$
$= b's'L^2$

Multiplying (21) and (22) gives the total volume of the locomotor musculature:

(23) volume of locomotor musculature $= vL \cdot b's'L^2$.

Let the mechanical power output per unit volume of locomotor musculature *when contracting* to produce the maximal speed be P. Then at maximal speed, by equation (23):

(24) mechanical power produced $= \frac{P}{2} \cdot vL \cdot b's'L^2$.

(The factor $\frac{1}{2}$ is introduced because only $\frac{1}{2}$ the musculature contracts at a time.)

To calculate the power required we need the following:

$$\text{frictional drag} = c_f \tfrac{1}{2}\rho A U^2 \cong c_f \tfrac{1}{2} A U^2$$

since $\rho \cong 1$ as in Bainbridge (1961) where c_f = coefficient of frictional drag and A = total surface area of the fish. Bainbridge states for most fish

$$\text{total drag} \cong 1.2 \times \text{frictional drag}.$$

A fish is not infinitely thin and hence builds up a pressure in front of itself by moving, a pressure drag, dependent on the shape of the fish, which must be added to the frictional drag to obtain the total drag.

If s is defined as the average depth of the fish divided by its length L (see Fig. 2), then the average depth of the fish is sL, and if the fish is not excessively rotund

$$A = 2 \cdot sL \cdot L.$$

Here the factor 2 indicates the fish has two lateral surfaces.

Combining the last three approximations:

(25) $$\text{total drag} \cong 1.2 \times \text{frictional drag}$$
$$\cong 0.6 c_f A U^2$$
$$\cong 1.2 \cdot sL^2 \cdot U^2 \cdot c_f$$

(26) $$\text{mechanical power required} = U \times \text{total drag}$$
$$\cong 1.2 \cdot sL^2 \cdot U^3 \cdot c_f.$$

The first equality is as in Bainbridge (1961), the second is from the final result of equation (25).

For laminar flow, where $p \cong 1$, the coefficient of frictional drag is

(27A) $$c_{f\,\text{lam}} = 1.328 R^{-1/2} = 1.328 \left(\frac{\rho L U}{\mu}\right)^{-1/2}$$
$$\cong 1.328\, \mu^{0.5} L^{-0.5} U^{-0.5}$$

and for turbulent flow is

(27B) $$c_{f\,\text{turb}} = 0.074 R^{-1/5} = .0.074 \left(\frac{\rho L U}{\mu}\right)^{-1/5}$$
$$\cong 0.074\, \mu^{0.2} L^{-0.2} U^{-0.2}$$

where R = Reynolds Number = $\frac{\rho L U}{\mu}$

μ = viscosity of the water

and the first equalities in each are from Bainbridge (1961).

Substituting (27A) and (27B) into (26) yields for laminar flow:

(28A) mechanical power required = $1.59 \cdot \mu^{0.5} \cdot s \cdot L^{1.5} \cdot U^{2.5}$

for turbulent flow

(28B) mechanical power required = $0.089 \cdot \mu^{0.2} \cdot s \cdot L^{1.8} \cdot U^{2.8}$.

The hydromechanical efficiency (η) is defined as previously

$$\eta = \frac{\text{mechanical power required}}{\text{mechanical power produced}}.$$

Substituting the expressions from (28A) and (28B) in turn along with that from (24) in the above definition of η yields

(29A) $$\eta = \frac{1.59 \cdot \mu^{0.5} \cdot s \cdot L^{1.5} \cdot U^{2.5}}{\frac{P}{2} \cdot \nu L \cdot b' s' L^2}$$

(29B) $$\eta = \frac{0.089 \cdot \mu^{0.2} \cdot s \cdot L^{1.8} \cdot U^{2.8}}{\frac{P}{2} \cdot \nu L \cdot b' s' L^2}$$

Solving (29A) and (29B) for U yields for laminar flow:

(30A) $$U_{\text{lam}} = 0.63 \cdot [\eta^{0.4}] \cdot \left[\frac{P^{0.4}}{\mu^{0.2}}\right] \cdot \left[\nu^{0.4} (b')^{0.4} \left(\frac{s'}{s}\right)^{0.4}\right] \cdot L^{0.6}.$$

for turbulent flow:

(30B) $$U_{\text{turb}} = 1.85 \cdot [\eta^{0.36}] \cdot \left[\frac{P^{0.36}}{\mu^{0.07}}\right] \cdot \left[\nu^{0.36} (b')^{0.36} \left(\frac{s'}{s}\right)^{0.36}\right] \cdot L^{0.43}.$$

These equations are a version of Bainbridge's final equations with which they agree well in power of L. The agreement would be exact if fish weight were proportional to length cubed rather than length to the 2.9 power as Bainbridge assumed. This discrepancy is predictable if there is systematic variation with L of some of the factors in the brackets, particularly for example some of the terms in the third set of brackets, containing the relative dimensions of the fish.

There are some corollaries of equations (30A) and (30B) because of the factors involved. All else remaining equal:

1) If a fish is hydrodynamically more efficient (larger η) it is faster.

2) Since viscosity (μ) is approximately doubled and power of fish muscle (P) is approximately halved in going from tropical to arctic waters, the net effect of colder temperatures is to decrease fish speed.

3) If a greater proportion of the fish's length is devoted to the locomotor spine (larger ν) the fish is faster.

4) If the breadth of the locomotor musculature (b') or the depth of the locomotor musculature relative to the total depth of the fish (s'/s) is increased, the fish is faster.

All of these corollaries are reasonable and lend credence to the approach taken.

Dependence of Thrust on Vertebral Number

The dependence of W_o, the maximal lateral velocity of the tail of the fish on the number of locomotor vertebrae (V), will now be demonstrated. The dependence of thrust on V will then follow from equation (20).

Lighthill (1970) assumed that the caudal motion of an anguilliform or carangiform fish was a sine-wave of constant amplitude traveling along the fish's body at a constant velocity (U_F). Mathematically speaking this assumption implies

(31) $W(x, t) = W_o \sin \omega (t + (L - x) U_F^{-1})$ near the tail.

All variables are here defined as in the previous section on Lighthill's model; x is the distance between the anterior tip of the fish and a variable point near the caudal end of the fish. When the sin = 1 this expression yields W_o, the maximal lateral velocity at the tail; the terms t and $(L - x)$ ensure sinusoidal variation in time and along the X-axis, respectively; the factor U_F^{-1} ensures that the propulsive wave travels along the fish with velocity U_F; and finally, ω is the angular velocity of the tail motion as defined by

$$\omega = 2\pi \cdot (\text{period of tail motion})^{-1}.$$

Let O, O' be points on the caudalmost vertebra as indicated in Fig. 3. If the caudalmost portion of the fish is roughly parallel to the X-axis as in Fig. 1, then the relative lateral velocity of O' about O will be well approximated by the difference in the lateral velocities of O and O'. Under these conditions

(32) relative velocity of O' about O $= W(x + dx, t) - W(x, t)$

where dx is as indicated in Fig. 2 and x is the distance from the anterior tip of the fish to O. (These variables and t are obviously not relative dimensions as are other lower case English script variables.)

As is shown in Appendix B

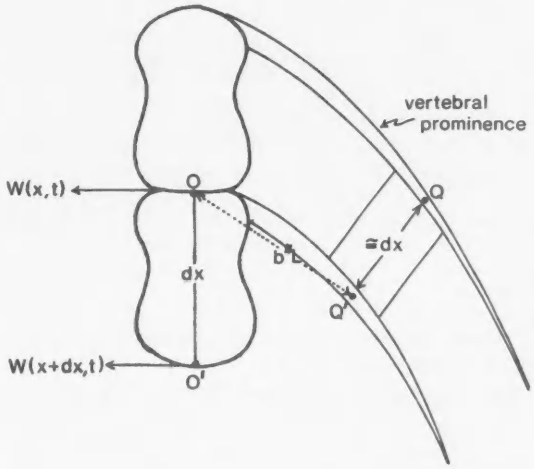
(33) $$[W(x + dx, t) - W(x, t)]_{\max} \cong \left[\frac{\partial W}{\partial x}\right]_{\max} dx$$

for any reasonably well-behaved function W.

From (31) by taking derivatives with respect to x

$$\frac{\partial W}{\partial x} = -W_o \cos \omega (t + (L - x) U_F^{-1}) \cdot \omega U_F^{-1}$$

The maximum of this quantity over time occurs when the tail of the fish is parallel to the X-axis as is shown in Appendix C. This is the same as the assumption that produced equation (32).



$$\text{Velocity } O' \text{ about } O = W(x+dx,t) - W(x,t)$$

$$\frac{b''L}{dx} = \frac{QQ'}{OO'} = \text{ratio of lever arms}$$

$$= \frac{\text{velocity of } Q' \text{ about } O}{\text{velocity of } O' \text{ about } O}$$

FIG. 3. Diagrammatic representation of dorsal perspective of caudalmost vertebra. See text for definition of symbols.

Since the maximum occurs when the cos $= -1$, we have for the right-hand side of equation (33):

$$(34) \qquad \left[\frac{\partial W}{\partial x}\right]_{\max} = W_o \cdot \omega U_F^{-1} = \frac{2\pi}{\lambda} W_o$$

where λ is the wavelength of the fish's motion near the tail (absolute and not relative to the length of the fish). The latter equality in (34) is a standard formula for wave motion from physics.

Substituting (34) into the right-hand side of equation (33) yields

$$(35) \qquad [W(x+dx,t) - W(x,t)]_{\max} \cong \frac{2\pi}{\lambda} \cdot W_o \cdot dx.$$

Considering the left-hand side of equation (35) we define (see Fig. 3): b" L = effective length of the lever arm on the prominence by which the muscles act on the caudalmost vertebra = OQ'. But

$$\frac{b''L}{dx} = \frac{OQ'}{OO'} = \text{ratio of lever arms}$$

$$= \frac{\text{speed of } Q' \text{ about } O}{\text{speed of } O' \text{ about } O}$$

since the speeds will be proportional to their respective lever arms. Taking advantage of equation (32) and solving the above equation for the speed of O' about O

$$W(x+dx,t) - W(x,t) = \frac{dx}{b''L} \cdot \text{speed of } Q' \text{ about } O.$$

Taking maxima of both sides

$$(36) \qquad [W(x+dx,t) - W(x,t)]_{\max} = \frac{dx}{b''L} \cdot \text{maximum speed of } Q' \text{ about } O.$$

The maximum speed of Q' about O is the maximum speed of shortening of the caudal musculature.

When the fish is moving at maximum speed, the maximum speed of shortening of muscle is related to the length of the muscle by

$$(37) \qquad \text{maximum speed of shortening} = \Sigma \cdot \text{length}.$$

The value of Σ will depend substantially on whether the caudal musculature is predominantly red or white and on whether the maximum speed referred to is burst or sustained.

Assuming the length of the muscle between the prominences (QQ' (Fig. 3)) is approximately dx, the length of caudal vertebrae, the maximum speed of muscle shortening is $\Sigma\, dx$, by (37). (If a muscle crosses a vertebral prominence without attaching, then it probably has about the same mechanical effect as one that does, since the overlying tissues will tend to strap it down to the vertebrae). If the velocity of Q' about O is in the same direction as the velocity of contraction of the vertebral musculature (which it should be for maximum mechanical efficiency), then the maximum speed of Q' about O is the maximum speed of muscle contraction and the maximum speed of Q' about O is $\Sigma\, dx$. Combining this with (36) yields:

$$(38) \qquad [W(x+dx,t) - W(x,t)]_{\max} = \frac{dx}{b''L} \cdot \Sigma\, dx$$

Combining equations (35) and (38) gives

$$\frac{2\pi}{\lambda} \cdot W_o \cdot dx = \frac{dx}{b''L} \cdot \Sigma\, dx$$

and solving for W_o yields

$$(39) \qquad W_o = \frac{\lambda}{2\pi} \cdot \Sigma \cdot \frac{dx}{b''L}.$$

An expression for dx, the length of the caudalmost vertebra must now be sought. The average length of locomotor vertebra is vL/V since this is just total length of the locomotor spine divided by the number of vertebrae; and c is defined as the ratio of the length of the caudalmost vertebra (dx) to the average length of the locomotor vertebrae. Then from the above:

$$(40) \qquad dx = c \cdot \frac{vL}{V}$$

Substituting for dx in (39) from (40) yields

$$(41) \qquad W_o = \frac{\lambda}{2\pi} \cdot \Sigma \cdot \frac{cv}{b''} \cdot \frac{1}{V}$$

Substituting for W_o in the equation for thrust (20) by means of the above equation gives

$$(42)\quad \text{thrust} = \tfrac{3}{4}S_o^2\cdot\left(\frac{\lambda^2}{4\pi^2}\cdot\Sigma^2\cdot\frac{c^2\nu^2}{(b'')^2}\cdot\frac{1}{V^2}\right)\cdot\eta(1-\eta)$$

$$= 0.019\cdot[\eta(1-\eta)]\cdot\left[\frac{c^2\nu^2}{(b'')^2}\cdot s_o^2\right]\cdot\Sigma^2\cdot\lambda^2\cdot\frac{L^2}{V^2}$$

where we have introduced s_o, the relative dimension of S_o, the depth of the tail of the fish, according to the formula

$$s_oL = S_o.$$

Equivalence of Thrust and Drag as a Constraint on Vertebral Number

Expressions for total drag in both laminar and turbulent flows are now derived and equated to the expression for thrust in equation (42). The resultant equations are solved for V and then U is eliminated through equations (30A) and (30B).

If the expressions for c_f from (27A) and (27B) are substituted into the expression for the total drag from (25) we have

$$(43A)\quad \text{total drag}_{\text{lam}} = 1.59\cdot\mu^{0.5}\cdot s\cdot L^{1.5}\cdot U_{\text{lam}}{}^{1.5}$$

$$(43B)\quad \text{total drag}_{\text{turb}} = 0.089\cdot\mu^{0.2}\cdot s\cdot L^{1.8}\cdot U^{1.8}{}_{\text{turb}}$$

Since thrust balances total drag at the maximum velocity (because the instantaneous acceleration must be zero, implying a balance of forces), these expressions must equal that for thrust from equation (42). Equating these expressions and solving for V^2 yields

$$(44A)\quad V^2{}_{\text{lam}} = 0.012\cdot[\eta(1-\eta)]\cdot\left[\frac{1}{\mu^{0.5}}\right]\cdot\left[\frac{c^2\nu^2}{(b'')^2}\cdot\frac{s_o^2}{s}\right]\cdot\Sigma^2\cdot\lambda^2\cdot L^{0.5}\cdot U_{\text{lam}}{}^{-1.5}$$

$$(44B)\quad V^2{}_{\text{turb}} = 0.21\cdot[\eta(1-\eta)]\cdot\left[\frac{1}{\mu^{0.2}}\right]\cdot\left[\frac{c^2\nu^2}{(b'')^2}\cdot\frac{s_o^2}{s}\right]\cdot\Sigma^2\cdot\lambda^2\cdot L^{0.2}\cdot U_{\text{turb}}{}^{-1.8}$$

and taking square roots yields

$$(45A)\quad V_{\text{lam}} = 0.11\cdot[\eta^{0.5}(1-\eta)^{0.5}]\cdot\left[\frac{1}{\mu^{0.25}}\right]\cdot\left[\frac{c\nu}{b''}\cdot\frac{s_o}{s^{0.5}}\right]\cdot\Sigma\cdot\lambda\cdot L^{0.25}\cdot U_{\text{lam}}{}^{-0.75}$$

$$(45B)\quad V_{\text{turb}} = 0.46\cdot[\eta^{0.5}(1-\eta)^{0.5}]\cdot\left[\frac{1}{\mu^{0.1}}\right]\cdot\left[\frac{c\nu}{b''}\cdot\frac{s_o}{s^{0.5}}\right]\cdot\Sigma\cdot\lambda\cdot L^{0.1}\cdot U_{\text{turb}}{}^{-0.9}$$

Substituting for U_{lam} and U_{turb} from (30A) and (30B) gives

$$(46A)\quad V_{\text{lam}} = 0.16\cdot[\eta^{0.2}(1-\eta)^{0.5}]\cdot\left[\frac{1}{P^{0.3}\mu^{0.1}}\right]\cdot\left[\frac{c\nu^{0.7}}{b''}\cdot\frac{1}{(b's')^{0.3}}\cdot\frac{s_o}{s^{0.2}}\right]\cdot\Sigma\cdot\lambda\cdot L^{-0.2}$$

$$(46B)\quad V_{\text{turb}} = 0.26\cdot[\eta^{0.18}(1-\eta)^{0.5}]\cdot\left[\frac{1}{P^{0.32}\mu^{0.04}}\right]\cdot\left[\frac{c\nu^{0.68}}{b''}\cdot\frac{1}{(b's')^{0.32}}\cdot\frac{s_o}{s^{0.18}}\right]\cdot\Sigma\cdot\lambda\cdot L^{-0.28}.$$

To derive these equations, no assumption has been made about the scaling of the variables on the right-hand side. Such assumptions (i.e. their dependence on the length L) will be made in the next section so that the comparison of the model with Lindsey's data and other empirical data may be facilitated.

Dependence on Length of Maximum Velocity of Muscle Contraction and Wavelength of Propulsive Wave

The two variables, Σ and λ, and their dependence on L are a potential major source of discrepancy between the model and nature. Data from Wardle (1975) and Webb (1977) are relevant and can be manipulated into approximate formulae for use in equations (46A) and (46B). These approximate formulae represent the variables Σ and λ in a qualitative fashion so that general trends in Lindsey's data may be predicted.

Σ the maximum speed of shortening per length muscle — According to Wardle (1975) the minimum twitch time (T), the time between stimulation and maximal contraction, of a block of teleost white lateral muscle $3.0 \times 1.5 \times 1.0$ cm^3, has a dependence on the length (L) of the fish it was taken from. With data derived from Wardle's graph, a functional regression with both variables logged yielded a slope of 0.37 and an $L = 1$ intercept of $T = 0.050$. Therefore the following is approximately true:

$$(47)\quad T = 0.050\,L^{0.37}$$

Assuming this relation is representative of all fish muscle and that fish muscle contracts down to 0.8 of its original length, then $\bar{\Sigma}$ as the average speed of shortening per unit length is

$$\bar{\Sigma} = \frac{0.2}{T} = 4.0L^{-0.37}$$

the last equality being due to equation (47).

If the velocity of muscle shortening is approximately sinusoidal with time then Σ, the *maximum* speed of shortening per unit length of muscle, is

$$(48)\quad \bar{\Sigma} = \frac{\pi}{2}\Sigma = 6.3L^{-0.37}$$

since the average of a sinusoidal function over a half cycle is $2/\pi$ times its maximum (see Appendix A).

λ — the absolute wavelength of the fish's motion — The other variable whose variation with L is well known is λ. Examining fig. 1 from Webb (1977) it was approximated that $\lambda/L \to 0.62$ as $L \to \infty$. Using the

data points from fig. 1 of Webb (1977) and functionally regressing log $(\lambda/L - 0.62)$ with log L yielded a slope of -1.4 and an $L = 1$ intercept of 2.10, hence

$$\lambda/L - 0.62 = 2.10L^{-1.4}$$

$$\lambda = 0.62L(1 + 3.4L^{-1.4}). \tag{49}$$

Substituting (48) and (49) into (46A) and (46B) and abbreviating everything between η and Σ with . . . , we have

$$V_{\text{lam}} = 0.62\cdot\ldots\cdot L^{0.43}(1 + 3.4L^{-1.4}) \tag{50A}$$

$$V_{\text{turb}} = 1.02\cdot\ldots\cdot L^{0.35}(1 + 3.4L^{-1.4}) \tag{50B}$$

It is thus apparent that the theoretical relation between log vertebral number and log length is not linear and that the slope of the linear regression will be strongly dependent on the range over which the variables are measured.

The Model and Lindsey's Data

The slopes for the regression of log V and log L from Lindsey (1975) range from -0.0704 to 0.4163. They cover a wide range and do not appear to provide verification for the theoretical slopes of equations (50A) and (50B). There are several contributing factors which are discussed below:

Lindsey's Method of Regression

Lindsey used a predictive regression of log V and log L. As Ricker (1973) suggests, in such situations a functional regression would be more appropriate. Regressing Y on X predictively gives slope

$$b = \Sigma xy/\Sigma x^2$$

The functional regression gives slope

$$v = \pm(\Sigma y^2/\Sigma x^2)^{1/2}$$

where the sign is the same as Σxy. Since the correlation coefficient is

$$r = \Sigma xy/(\Sigma x^2\cdot\Sigma y^2)^{1/2}$$

then

$$v = \frac{b}{r}$$

with the sign of v the same as b, r, and Σxy

Table 1 gives Lindsey's data with functional regression slopes inserted for comparison with the predictive regression slopes. The corrected slopes (v) for Lindsey's material are invariably larger in absolute value than those of Lindsey (1975) because the correlation coefficient is invariably ≤ 1 in absolute value. The functional slopes are also highly variable, from -0.4841 to $+0.5675$, the departures from theory apparently still being substantial.

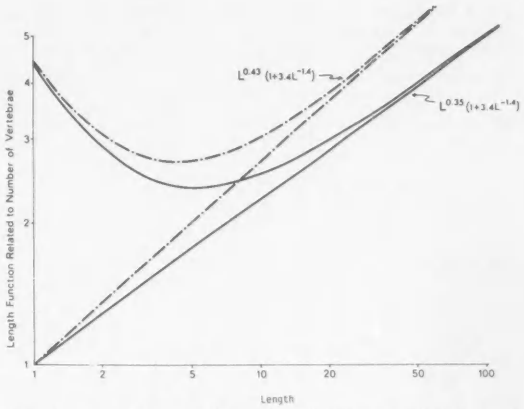


FIG. 4. Log–log graphs of $L^{0.35}(1 + 3.4\,L^{-1.4})$ and $L^{0.43}(1 + 3.4\,L^{-1.4})$ vs. L. The latter is dotted. Asymptotes $L^{0.35}$ and $L^{0.43}$ vs. L are also shown.

The Theoretical Relation is not Linear

As equations (50A) and (50B) indicate, the theoretical relation between log (V) and log (L) is not linear. From these equations it would be predicted that the slopes of the functional regressions for Lindsey's data would vary from negative values where the lengths cover a small range of low values, to positive values with slopes as high as 0.43 where the lengths are in a small range of high values. Generally speaking, this is a good description of the functional regression slopes in Table 1.

To illustrate, graphs of $L^{0.43}(1 + 3.4\,L^{-1.4})$ and $L^{0.35}(1 + 3.4\,L^{-1.4})$ vs. L on log–log axes are given in Fig 4. The slopes of V_{lam} and V_{turb} vs. L for $L > 10$ cm are close to 0.43 and 0.35, but if the range of L were to include points for which $L < 10$ cm, then regression lines through the data points would yield slopes substantially <0.43 and 0.35, and perhaps even negative slopes.

On this basis one would expect a positive correlation between log minimum length in the data considered and the slope of the log–log functional regression. This does indeed occur (Table 2). As can be seen, the correlation of slope and log minimum length is consistently greater than those of slope and log mean or log maximum length. (The large negative correlation between slope and log of the length range, i.e. log (maximum length/minimum length), is perhaps a reflection of the positive one between slope and log min length.) Similarly, one would expect that in the absence of fish of small length, there would be a positive correlation between slope of the log–log functional regression and the minimum vertebral number, and increasingly greater positive correlations with mean and maximum vertebral number, both of which occur consistently in Table 2. A confounding factor is the effect of structural vertebrae which is discussed further below. These relationships

TABLE 1. Slopes of predictive and functional regressions in the relation between vertebral number and length and related statistics for various families of fishes. Column Sig indicates statistical level of significance of the functional regression, viz: 1 = $P < 0.001$, 2 = 0.001–0.01, 3 = 0.01–0.02, 4 = 0.02–0.05, 5 = $P > 0.05$ (data from Lindsey 1975).

Family		Pred slope	Functional slope	Intcpt	Vertebrae			Length			No. of species	r	Sig
No.	Name				Mean	Min	Max	Mean	Min	Max			
150	Petromyzontidae	0.1115	0.1841	32.53	60.02	51.00–	71.50	27.83	13.00–	89.00	17	0.6056	2
890	Scyliorhinidae	0.1489	0.2552	46.57	134.49	109.00–	186.00	63.76	30.20–	304.00	12	0.5834	4
900	Carcharhinidae	0.1738	0.2490	48.99	168.83	114.70–	244.60	143.98	24.20–	1049.00	56	0.6981	1
910	Sphyrnidae	0.2490	0.2976	30.30	176.82	120.00–	205.50	375.34	152.40–	1059.00	6	0.8367	4
930	Squalidae	0.2329	0.3115	25.68	94.26	60.00–	126.00	65.02	12.80–	200.00	24	0.7477	1
990	Rajidae	0.2595	0.5134	9.59	90.46	65.80–	122.40	79.25	36.90–	151.00	23	0.5055	3
1920	Clupeidae	0.1082	0.1591	28.96	46.12	37.00–	61.00	18.64	3.50–	76.00	139	0.6802	1
1930	Engraulidae	0.1251	0.2580	23.13	43.67	38.00–	75.50	11.73	3.30–	60.00	74	0.4848	1
2050	Coregonidae	0.0657	0.1113	38.77	59.46	53.20–	66.60	46.66	16.70–	152.00	32	0.5904	1
2051	Salmonidae	0.0353	0.1082	38.69	62.78	54.50–	69.50	87.67	14.10–	155.10	19	0.3262	5
2090	Osmeridae	0.1018	0.1682	37.39	62.11	54.50–	68.50	20.45	9.80–	40.00	11	0.6053	4
2100	Argentinidae	0.1703	0.2614	21.92	48.28	40.50–	66.00	20.51	11.30–	55.00	9	0.6514	4
2110	Bathylagidae	0.0140	0.2491	24.61	47.54	41.00–	54.00	14.06	9.10–	21.50	12	0.0562	5
2140	Salangidae	0.3608	0.3782	27.40	64.55	50.90–	73.50	9.64	6.00–	13.70	5	0.9539	2
2200	Esocidae	0.2161	0.2310	19.69	57.16	46.40–	65.00	100.85	38.00–	182.00	5	0.9353	2
2210	Gonostomatidae	0.0650	0.2114	25.25	40.82	31.50–	63.00	9.70	3.10–	61.00	23	0.3075	5
2220	Sternoptychidae	0.1527	0.2137	23.78	34.99	29.50–	39.00	6.09	2.60–	10.50	12	0.7146	2
2230	Stomiatidae	0.4163	0.5298	13.70	60.38	39.00–	164.00	16.44	5.30–	43.00	18	0.7858	1
2260	Melanostomiatidae	0.0620	0.1875	32.61	53.64	44.00–	65.00	14.21	4.90–	32.30	18	0.3306	5
2420	Synodontidae	0.1576	0.2401	23.31	54.30	44.00–	63.00	33.83	9.80–	64.00	14	0.6563	2
2470	Paralepididae	−0.0469	−0.2651	167.62	81.77	59.50–	116.00	14.99	4.50–	49.50	21	−0.1769	5
2500	Myctophidae	−0.0260	−0.1357	50.22	37.23	33.00–	41.00	9.07	2.60–	19.00	16	−0.1916	5
2600	Mormyridae	0.1648	0.2218	22.62	47.59	38.10–	64.00	28.60	9.20–	120.00	32	0.7430	1
2610	Characidae	0.1170	0.1312	27.41	39.14	34.00–	50.00	15.10	2.10–	80.00	24	0.8915	1
2660	Citharinidae	0.0487	0.1165	29.68	40.98	30.00–	50.00	15.98	2.30–	84.00	26	0.4182	4
2710	Catostomidae	0.0231	0.1510	23.97	42.38	35.50–	51.00	43.54	15.00–	104.00	25	0.1530	5
2720	Cyprinidae	0.1051	0.3394	15.02	40.12	28.00–	58.00	18.09	2.80–	122.00	272	0.3097	1
2830	Bagridae	0.0006	0.1154	29.30	45.36	41.00–	54.20	44.12	8.00–	100.00	11	0.0052	5
2850	Ictaluridae	0.1085	0.1283	26.73	37.31	31.30–	52.00	13.46	4.00–	132.00	32	0.8458	1
2950	Mochokidae	0.1059	0.1302	25.20	37.62	30.80–	44.00	21.72	3.10–	47.00	17	0.8133	1
3190	Congridae	0.0645	0.1512	75.96	139.83	115.00–	160.50	56.66	14.30–	240.00	26	0.4267	4
3350	Belonidae	0.1278	0.1390	44.63	76.86	53.50–	91.50	49.91	4.00–	152.00	9	0.9195	1
3380	Exocoetidae	0.1857	0.2745	17.85	44.33	36.50–	51.50	27.49	14.20–	48.50	170	0.6764	2
3400	Moridae	0.1485	0.2865	18.62	54.79	52.00–	59.90	43.22	34.00–	66.00	12	0.5183	5
3420	Gadidae	0.1202	0.2326	20.74	54.36	42.00–	82.00	62.90	15.00–	200.00	36	0.5167	2
3540	Syngnathidae	0.2074	0.3846	18.95	55.09	27.50–	111.50	16.02	3.20–	60.00	113	0.5392	1
3620	Cyprinodontidae	0.1497	0.2205	21.21	30.63	24.60–	37.00	5.29	2.10–	15.00	27	0.6789	1
3670	Poeciliidae	0.0073	0.1287	24.44	30.54	28.00–	34.30	5.64	2.00–	13.00	34	0.0567	5
3920	Sphyraenidae	0.0000	0.0000	24.00	24.00	24.00–	24.00	64.18	30.00–	183.00	11	0.0000	5
3940	Atherinidae	0.1208	0.1710	27.68	43.21	31.00–	52.00	13.51	5.00–	46.00	26	0.7064	1
4000	Centropomidae	0.0137	0.0180	22.51	24.18	24.00–	25.00	52.76	18.00–	320.00	16	0.7597	1
4010	Serranidae	−0.0121	−0.0344	27.45	24.33	24.00–	26.00	33.59	3.00–	229.00	75	−0.3522	2
4011	Percichthyidae	−0.0331	−0.1555	50.79	27.76	25.00–	35.90	48.69	8.00–	263.00	23	−0.2129	5
4090	Centrarchidae	0.0862	0.1033	21.96	30.05	24.50–	33.00	20.82	3.00–	63.50	26	0.8345	1
4130	Percidae	0.0530	0.1010	31.16	39.45	33.00–	48.00	10.33	4.00–	137.00	65	0.5247	1
4220	Carangidae	0.0072	0.0379	20.97	24.25	24.00–	26.00	46.54	19.90–	183.00	29	0.1902	5
4260	Bramidae	−0.0089	−0.0976	61.40	42.55	40.00–	51.20	42.87	8.90–	122.00	10	−0.0912	5
4310	Lutjanidae	−0.0139	−0.0286	26.62	24.06	23.60–	26.00	34.36	9.00–	91.50	26	−0.4862	3
4350	Pomadasyidae	0.0057	0.1210	16.89	25.77	24.00–	27.00	32.84	20.00–	60.00	12	0.0471	5
4360	Sciaenidae	−0.0099	−0.0572	30.35	24.66	23.00–	28.00	37.71	8.70–	190.00	48	−0.1730	5
4380	Sparidae	0.0000	0.0000	24.00	24.00	24.00–	24.00	44.17	28.00–	90.00	14	0.0000	5
4470	Kyphosidae	0.0205	0.0216	24.75	26.87	26.50–	27.00	44.28	24.00–	64.50	4	0.9473	3
4580	Cichlidae	−0.0039	−0.1327	43.29	29.86	25.70–	38.00	16.45	6.60–	75.00	76	−0.0294	5
4600	Embiotocidae	−0.0565	−0.4841	150.87	27.12	31.00–	38.10	34.63	14.90–	58.00	21	−0.1167	5
4620	Labridae	−0.0049	−0.2300	63.62	28.39	23.00–	41.00	33.36	5.00–	214.00	44	−0.0213	5
4940	Blenniidae	0.0103	0.1070	28.26	34.63	29.80–	41.00	6.68	2.20–	34.00	50	0.0963	5
5010	Clinidae	0.1121	0.2067	25.08	41.67	32.00–	57.00	11.67	3.50–	61.00	19	0.5424	3
5030	Stichaeidae	0.0941	0.2565	29.64	65.97	43.00–	82.50	22.62	7.50–	76.50	20	0.3668	5

TABLE 1 (*Concluded*)

Family No.	Family Name	Pred slope	Functional slope	Intcpt	Vertebrae Mean	Vertebrae Min	Vertebrae Max	Length Mean	Length Min	Length Max	No. of species	r	Sig
5040	Pholidae	0.1576	0.3679	27.99	86.44	61.00–	105.70	21.44	9.50–	46.00	12	0.4284	5
5060	Microdesmidae	0.2459	0.3139	26.03	54.40	41.50–	63.20	10.47	6.00–	25.70	10	0.7834	2
5080	Zoarcidae	0.0296	0.0948	75.71	104.49	83.50–	147.00	29.92	10.90–	74.50	21	0.3123	5
5150	Ophidiidae	0.1938	0.3569	19.65	58.02	40.00–	87.90	20.77	8.90–	46.00	16	0.5430	4
5170	Ammodytidae	0.1709	0.2584	30.52	67.28	56.00–	74.30	21.30	11.40–	35.00	10	0.6613	4
5240	Trichiuridae	0.3220	0.5675	9.19	112.14	58.00–	191.00	82.08	20.40–	183.00	13	0.5674	4
5250	Scombridae	0.1439	0.2626	12.32	39.29	31.00–	60.00	82.85	18.80–	300.00	40	0.5480	1
5340	Stromateidae	0.0782	0.3589	10.02	31.01	25.00–	46.00	23.31	8.00–	50.80	21	0.2179	5
5350	Nomeidae	−0.0707	−0.1750	53.98	30.79	26.00–	41.00	24.73	3.70–	122.00	19	−0.4040	5
5360	Anabantidae	0.0199	0.0869	22.07	27.08	25.00–	30.50	10.51	3.50–	61.00	17	0.2289	5
5410	Gobiidae	−0.0194	−0.1636	43.82	29.64	25.00–	37.50	10.91	2.50–	61.00	36	−0.1186	5
5440	Scorpaenidae	0.0514	0.2951	9.94	26.16	23.00–	30.50	26.60	4.90–	92.00	119	0.1742	5
5450	Triglidae	−0.0472	−0.2044	71.25	33.83	27.00–	37.00	38.23	15.20–	61.00	11	−0.2309	5
5500	Hexagrammidae	0.2253	0.3198	15.04	50.96	37.50–	61.00	45.47	25.50–	152.00	13	0.7046	2
5550	Icelidae	−0.0069	−0.1208	48.65	34.91	32.90–	38.30	15.60	8.50–	27.00	11	−0.0571	5
5560	Cottidae	0.0656	0.2077	19.46	34.62	24.00–	55.00	16.01	5.10–	63.50	90	0.3159	2
5570	Cottocomephoridae	0.0938	0.1379	22.59	32.50	29.00–	36.00	14.00	5.50–	22.50	11	0.6802	3
5620	Agonidae	0.0144	0.2707	18.25	39.59	35.50–	46.00	17.47	9.00–	31.00	15	0.0532	5
5630	Cyclopteridae	0.0704	0.0875	21.73	27.20	23.50–	29.00	13.02	3.90–	61.00	10	0.8047	2
5631	Liparidae	0.1533	0.4363	14.77	51.38	35.20–	70.00	17.41	5.90–	46.00	17	0.3514	5
5680	Bothidae	0.0169	0.1965	21.29	38.25	33.00–	55.00	19.71	6.60–	152.00	90	0.0860	5
5690	Pleuronectidae	0.1304	0.3379	11.23	41.68	29.00–	64.20	48.43	13.00–	266.70	46	0.3859	2
5700	Soleidae	0.0574	0.4127	10.31	33.55	24.00–	49.70	17.47	7.00–	51.00	30	0.1391	5
5810	Balistidae	−0.0278	−0.1451	32.94	19.84	17.00–	23.00	32.94	6.00–	101.00	14	−0.1916	5
5830	Tetraodontidae	0.0373	0.1459	11.30	18.70	17.00–	22.00	31.66	11.50–	76.00	22	0.2557	5
5860	Gobiesocidae	−0.0376	−0.2264	44.27	31.19	26.00–	43.00	4.70	2.10–	30.00	32	−0.1661	5
5870	Batrachoididae	0.2396	0.3088	14.33	32.89	26.50–	47.60	14.75	5.40–	48.50	11	0.7759	2

are of course only useful in drawing qualitative conclusions, for the various families have been given equal weight in the correlations while the statistics for each are based on a varying number of species. They nevertheless provide a good rationale for the wide range of functional regression slopes for Lindsey's data.

LOCOMOTOR AND STRUCTURAL VERTEBRAE

The theory underlying the model only provides a relationship between V, the *locomotor vertebrae*, and L, the length, whereas the total numbers of vertebrae, $V_o + V$, (i.e. structural plus locomotor) were recorded by Lindsey. Figure 5 shows the effect that structural vertebrae would have on the analysis if their number were constant at V_o for a given family of fish. As would be expected from their constant numbers, the structural vertebrae influence the theoretical relation between log vertebral number and log length in such a way as to give greatest departures from predicted values at the smaller values of total vertebral number which correspond to smaller lengths.

TABLE 2. Correlations between slope of the log–log functional regressions and the log of the maximum, mean, minimum, and range of length and the log of the maximum, mean, minimum, and range of vertebral number, for 85 families of fishes, 17 families of anguilliform fishes, and 60 families of carangiform fishes (data from Lindsey 1975).

	Number of families	Maximum	Mean	Minimum	Range
Correlation coefficient between slope and logarithm of length					
Grouped	85	−0.0187	0.0800	0.1724	−0.1985
Anguilliform	17	0.1346	0.3778	0.4825	−0.4387
Carangiform	60	−0.0543	−0.0021	0.0826	−0.1277
Correlation coefficient between slope and logarithm of vertebral number					
Grouped	85	0.5251	0.4753	0.3484	0.5274
Anguilliform	17	0.4300	0.3523	0.1641	0.6803
Carangiform	60	0.3609	0.3312	0.1986	0.4073

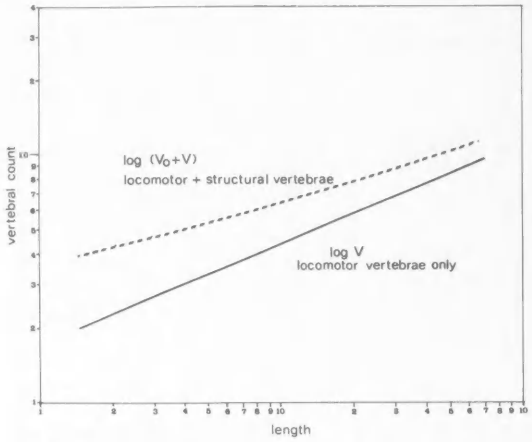


FIG. 5. Effect of structural vertebrae on the relation between log vertebral count and log length.

The slope of a linear regression using total vertebral counts is, therefore, less than that for an expression using only the locomotor vertebrae. The smaller observed slopes should belong to the families with smaller ranges and larger numbers of structural vertebrae.

This may account for Lindsey's observation that viviparous fish have lower slopes than corresponding egg-laying families, if it is true that viviparous families of fish have more structural vertebrae than their egg-laying counterparts.

It is also worth remarking that the carangiform swimmers have a greater proportion of structural vertebrae than anguilliforms. Accordingly, it would be expected that the anguilliforms would show greater slopes in the relation of vertebral count to length and in general they do (Table 1).

This phenomenon also suggests that there should be a correlation between the log of the family mean vertebral number and the slope, since with high vertebral counts the actual and theoretical slopes are in better agreement. One would also predict an even better correlation between slope and ranges of the logs of the vertebral counts, because the increase in vertebral count is attributed to locomotor vertebrae. This is also seen in Table 2.

As a final note, observed slopes would still be smaller than the theoretical slopes even if the number of structural vertebrae, V_o, increased with length, as long as their number did not increase with length as fast as the number of locomotor vertebrae.

THE LINE THROUGH LINES EFFECT

Derived equations for dependence of vertebral count on length do not allow for a negative slope between log V and log L except over a very small range of low

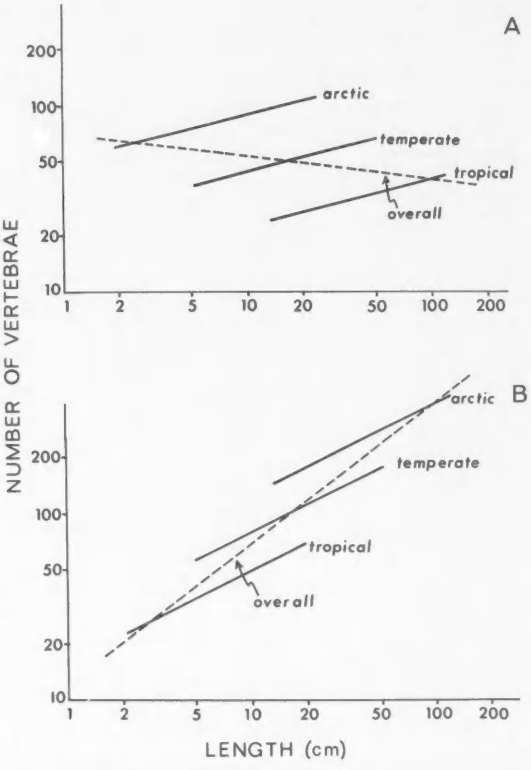


FIG. 6. "Line through lines effect." Solid lines are data regressed by temperature zones; dotted lines represent regression lines through all data points.

lengths, but they do provide for an effect of temperature on vertebral counts. Lindsey's only temperature data are given in his Fig. 3. As can be observed there for the Labridae, the slopes of the predictive regressions within temperature zones are positive but when aggregated, the data yield a regression line with negative predictive slope.

The potential variability of this effect is illustrated in Fig. 6, in which the solid lines in A and B represent regression lines restricted to temperature zones while the dotted lines represent regression lines through all data points. The direction of change in slope of the regression line is dependent on which species are included from which zones. It is this effect that forms the most serious objection to testing of the model by means of Lindsey's data and no more than rough agreement should be expected.

OTHER CONSIDERATIONS

Equations (46A) and (46B) contain factors for relative dimensions (the terms in the third set of square

brackets). Concerning relative dimensions, Lindsey observes: "The extent to which individual species depart from the overall correlation within a family is attributable in part to the degree of their dissimilarity in body form . . ." (p. 2455, col. 2), and he notes as an impression, that rotund and deeper forms tend to have fewer vertebrae.

If a more rotund form within a family tends to have broader spinal musculature, then b' and b'' would be greater and equations 46A and 46B translate this as implying fewer vertebrae.

A problem occurs in the interpretation of the depth effect. On superficial inspection it appears that equally increasing the depth factors s_o, s, s' would increase rather than decrease the number of vertebrae. There are two possible explanations for the depth effect: either deeper fish tend to be broader and hence the factors $(b')^{0.3}$ and b'' in the denominators increase and compensate for the effect of the depth variables, or else the depth increase affects s_o less than s or s'. The latter possibility is attractive for if an increase in depth across a family of fish is due mostly to an increase in spinal muscle depth, s_o should increase more slowly than s or s', and fewer vertebrae would result.

Bearing in mind the various shapes that different families of fish assume and the modifications of shape that occur within families, it is to be expected that there might be substantial and complicated modifications of the relation between vertebral count and length as described by equations (46A) and (46B).

Equations (46A) and (46B) also contain a factor dependent on temperature (the terms in the second set of square brackets). Between tropical and arctic waters μ (viscosity) is doubled while P (ratio of power to volume of muscle) is halved. The effect on Σ (ratio of muscle velocity to length) and other variables is unknown. If most of power loss between tropical and arctic water is due to slower shortening, i.e. Σ is halved, then (46A) and (46B) would tend to indicate that vertebral number would decrease as the waters became colder. This is in disagreement with Jordan's Rule. There are, however, many variables in these equations, any of which may vary systematically with the temperature. There are many difficulties but variations of vertebral number with temperature are implied by (46A) and (46B) and may provide a theoretical basis for Jordan's Rule.

Stride Length of Fish Motion

The foregoing theory can also be used to derive a relationship between stride length and fish length:

$$\text{stride length} = 2UT$$

where, as before, U = max velocity, T = twitch time which Wardle (1975) assumed was one half the period of motion of the fish's tail.

By equation (30A):

$$U_{\text{lam}} \alpha L^{0.6}$$

By Wardle's data, equation (47):

$$T \alpha L^{0.37}$$

and therefore in theory:

$$\text{stride length } \alpha L^{0.97} \text{ for laminar flow.}$$

Using equation (30B) to get U_{turb} yields

$$\text{stride length } \alpha L^{0.8} \text{ for turbulent flow.}$$

Wardle (1975) gives the empirically derived relation

stride length is proportional to L with proportionality constant 0.6–0.8

A calculation of the constant of proportionality for the theoretical equations involves making too many assumptions about constants in (30A) and (30B) to be useful. Rough calculations tend to yield constants too large by about a factor of 10 but the agreement between actual and theoretical exponents is still striking.

Discussion

Lindsey (1975) made a number of suggestions for possible causes of pleomerism, among which he gave considerable attention to hydrodynamical considerations. From the foregoing it would seem pleomerism can indeed be largely related to swimming efficiency. There is a modest measure of agreement between the predictions from a hydrodynamical model, and the observed relations between vertebral count and length. Additionally, the model here presented provides corollary predictions on such matters as the effect of temperature on vertebral counts, the effect of changes in shape and the significance of the type of swimming motion as it is related to the proportions of structural and locomotor vertebrae. It also provides a theoretical basis for an empirical observation on stride length.

The basic premise of an hydrodynamical model of pleomerism must be that selective factors have favored fish with vertebral counts that are consistent with efficiency in swimming. If one accepts the view that predation is an important factor in selection, which seems reasonable, it is equally reasonable to question whether maximum length is an appropriate measure of the effect of selective processes. Virtually all species of fish begin life small enough to be victims of predation, and some are victimized throughout their lifetimes while achieving maximum length. On the other hand, most species of fish are predators on something, and their swimming speed is a factor in the success of feeding over the whole life span. At best then, maximum length is probably a weak correlate of the length at which selection would be concentrated.

If an attempt to disprove the thesis of this paper were to be made, equations (46A) and (46B) are the key about which data should be collected. Ideally the family to which the data pertains should have a large size range

(including fish of length <10 cm) but similar shapes (otherwise collection of data on relative dimensions would be preferable). The data would have to be stratified by temperature zones. Data on variation of Σ and λ with L for this family would also be required.

Acknowledgments

The research on which this paper is based was prompted by a comment on a reprint of Lindsey (1975), which Lindsey sent to P.A.L. The comment read, "Kindly give me the reason for all this." It is, accordingly, appropriate to acknowledge Dr Lindsey's stimulus as the reason for this attempt to provide a reason for pleomerism. The mathematical analysis of this paper is the work of J.L.S.; P.A.L. contributed some orientation, statistical comments, and editorial experience. Mr W. Gazey provided useful advice on regressions, and Dr J. D. McPhail and Dr N. J. Wilimovsky provided advice on ichthyological matters. As referees on the first draft of this paper, Dr C. C. Lindsey and Dr P. W. Webb made a number of very valuable suggestions. The research was supported from a grant from the National Research Council of Canada.

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Appendix A. Average values for Sinusoidal Functions

Given that

$$Y = Y_o \sin \omega t \quad \text{when} \quad Y_o = \text{maximum of } Y,$$

the average value of Y over its positive values, $\bar{Y}$, is

$$\begin{aligned}\bar{Y} &= \frac{1}{\tau_o}\int_o^{\tau_o} Y_o \sin \omega t\, dt \quad \text{where} \quad \omega\tau_o = \pi \\ &= \frac{1}{\tau_o}\left[-Y_o \cos \omega t \cdot \frac{1}{\omega}\right]_o^{\tau_o} \\ &= \frac{Y_o}{\omega\tau_o}[1 - \cos \omega\tau_o] = \frac{Y_o}{\pi}[1 - \cos \pi] \\ &= \frac{2}{\pi} Y_o.\end{aligned}$$

The average value of Y^2 is

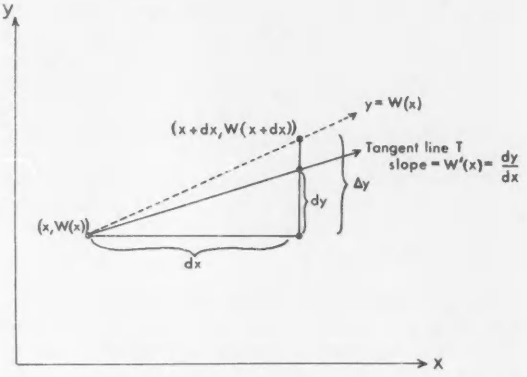

FIG. 7. Graph of $y = W(x)$ and its tangent line illustrating that $\Delta y \cong dy$.

$$\begin{aligned}\bar{Y}^2 &= \frac{1}{\tau_o}\int_o^{\tau_o} Y_o^2 \sin^2 \omega t\, dt \quad \text{where} \quad \omega\tau_o = \pi \\ &= \frac{Y_o^2}{\tau_o}\int_o^{\tau_o} \sin^2 \omega t\, dt \\ &= \frac{Y_o^2}{\tau_o}\int_o^{\tau_o} \frac{1 - \cos 2\omega t}{2}\, dt \\ &= \frac{Y_o^2}{\tau_o}\left[\frac{t}{2} - \frac{\sin 2\omega t}{4}\right]_o^{\tau_o} \\ &= \frac{Y_o^2}{\tau_o}\left[\frac{\tau_o}{2} - \frac{\sin 2\omega\tau_o}{4}\right] \\ &= \frac{Y_o^2}{\tau_o}\left[\frac{\tau_o}{2} - \frac{\sin 2\pi}{4}\right] = \frac{Y_o^2}{\tau_o}\frac{\tau_o}{2} \\ &= \frac{Y_o^2}{2}.\end{aligned}$$

Appendix B. Approximation of $[W(x + dx, t) - Wx, t]_{\max}$

From Fig. 7 which diagrammatically represents $W(x, t)$:

(51) $$\Delta y \cong dy$$

$$\Delta y = W(x + dx) - W(x)$$

$$\frac{dy}{dx} = W'(x) \quad \text{or} \quad dy = W'(x)dx.$$

Substituting for the two sides of (51) from these equations

$$W(x + dx) - W(x) \cong W'(x)dx.$$

We now acknowledge that W has a dependence on time (t)

$$W(x + dx, t) - W(x, t) \cong \frac{\partial W}{\partial x}\, dx$$

($W'(x)$ becomes $\partial W/\partial x$, the partial derivative with respect to x, because W varies with x and an additional

variable, time, t, which must be held constant. Denoting the maximum of a bracketed quantity with respect to time by the subscript max, we have from the above equation

$$[W(x + dx, t) - W(x, t)]_{\max} \cong \left[\frac{\partial W}{\partial x}\right]_{\max} dx.$$

Appendix C. Parallelism Conditions

If the caudal portion of the fish is parallel to the X axis then mathematically

$$\frac{\partial h}{\partial x} = 0 \text{ at the tail}$$

where h = lateral displacement of the body from the X axis. But

$$\frac{\partial h}{\partial x} = -\frac{\partial h}{\partial t}\Big/\frac{\partial x}{\partial t} = -W(x, t)\Big/U_F$$

The first equality is from standard multivariable calculus, the second, the definition of W and U_F. The parallelism of the tail is therefore equivalent to

$$W(x, t) = 0 \quad \text{at the tail} \tag{52}$$

If $\partial W/\partial x$ is at a maximum with respect to time t (i.e. for $[\partial W/\partial x]_{\max}$), then the derivative of this variable with respect to time is zero, i.e.

$$\frac{\partial}{\partial t}\left(\frac{\partial W}{\partial x}\right) = 0 \tag{53}$$

Using equation (31) gives:

$$\begin{aligned}\frac{\partial}{\partial t}\left(\frac{\partial W}{\partial x}\right) &= \frac{\partial}{\partial t}\left[\frac{\partial}{\partial x}(W_o \sin \omega(t + (L - x)U_F^{-1})\right] \\ &= \frac{\partial}{\partial t}[W_o \cos \omega(t + (L - x)U_F^{-1})\cdot\omega U_F^{-1}][-1] \\ &= W_o \sin \omega(t + (L - x)U_F^{-1})\cdot\omega^2 U_F^{-1} \\ &= W(x, t)\cdot\omega^2 U_F^{-1}\end{aligned}$$

Hence, for $[\partial W/\partial x]_{\max}$, equation (53) and the above imply equation (52), the parallelism condition.

Concentrations of Cd, Cu, Mn, Pb, and Zn in Fishes in a Highly Organic Softwater Pond

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WIENER, J. G., AND J. P. GIESY JR. 1979. Concentrations of Cd, Cu, Mn, Pb, and Zn in fishes in a highly organic softwater pond. J. Fish. Res. Board Can. 36: 270–279.

Concentrations of Cd, Pb, and three essential metals (Cu, Mn, and Zn) in stocked bluegill (*Lepomis macrochirus*) and eight resident species of fish were studied in an acidic, highly organic pond on the southeastern U.S. coastal plain. Concentrations of Cu, Mn, and Zn in stocked and resident fish were apparently homeostatically controlled in liver tissue, axial musculature, and whole body. Concentrations of all metals studied in axial muscle tissue and whole body of stocked bluegill remained relatively constant after 200 d of residence in the pond. Analysis of concentration factors from pond water to whole stocked bluegill indicated that Pb in this system was less available to fish than in hardwater lakes. In contrast, Cd in the pond was as available to fish as in harder waters. Differences in relative availabilities of Cd and Pb were explained by the tendency of Pb to form complexes with naturally occurring organics. The need for metal-specific analysis of biological availability of metals in highly organic softwater systems is stressed.

Key words: trace metal, availability, fish, soft water, concentration factor, organic water

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Nous avons étudié les concentrations de Cd, Pb et trois métaux essentiels (Cu, Mn et Zn) dans des crapets arlequins introduits et huit espèces de poissons résidentes dans un étang acide, fortement organique, de la plaine côtière du sud-est des É.-U. Les concentrations de Cu, Mn et Zn dans les poissons introduits et résidents sont apparemment contrôlées homéostatiquement dans le tissu hépatique, la musculature axiale et le corps entier. Les concentrations de tous les métaux étudiés dans le tissu du muscle axial et dans le corps entier des crapets arlequins introduits sont demeurées relativement constantes après 200 jours de résidence dans l'étang. Une analyse des facteurs de concentration entre l'eau de l'étang et les crapets arlequins introduits entiers indique que le Pb dans ce réseau est moins accessible aux poissons que dans les lacs d'eau dure. Par contraste, le Cd dans l'étang est aussi accessible aux poissons que dans les eaux plus dures. Nous expliquons les différences dans la disponibilité relative du Cd et du Pb par la tendance du Pb à former des complexes avec des matières organiques présentes naturellement. Nous soulignons le besoin d'une analyse, métal par métal, de la disponibilité biologique des métaux dans des réseaux d'eau douce, fortement organique.

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AVAILABILITY and toxicity of trace metals to aquatic biota are primarily determined by the chemical nature of the aquatic environment. Most investigations of trace metal dynamics and bioavailability in freshwaters have been conducted in hardwater systems in which inorganic ligands, usually carbonate (Pagenkopf et al. 1974), control toxicity and availability of metals to biota. Freshwaters of the U.S. southeastern coastal plain are characterized by low alkalinity, hardness, and pH and high concentrations of dissolved humic and fulvic acids (Beck et al. 1974). Relatively few investigations of trace metal dynamics have been conducted in acidic, highly organic waters and few of these have attempted to assess availability of trace metals to biota. Because naturally occurring organic acids can affect both toxicity and availability of trace metals to biota (Zitko et al. 1973; Brown et al. 1974; Milanovich et al. 1975; George and Coombs 1977; Giesy et al. 1977), information on availability of metals in these systems is essential.

The primary objective of this study was to compare availability to fish of selected trace metals in an acidic, highly organic pond (Skinface Pond) with availability in hardwater systems. Five metals, Cd, Cu, Mn, Pb, and Zn, were studied. Copper, Mn, and Zn are essential trace metals and are presumably homeostatically controlled (Bowen 1972; Frieden 1972; Cross et al. 1973; Bryan 1976; Giesy and Wiener 1977). Cadmium and Pb are nonessential, toxic metals (Davies et al. 1976;

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Fleischer et al. 1974). Although essential, Cu and Zn can be acutely toxic at higher concentrations (Skidmore 1964; Black et al. 1976). Manganese is relatively nontoxic to aquatic biota and is seldom a problem in freshwaters (USEPA 1975). Analyses of these metals were conducted on eight species of resident fishes from the pond and on stocked bluegill (*Lepomis macrochirus*) that were collected at various time intervals following release into Skinface Pond. Comparison of availability was accomplished by analysis of *concentration factors*. However, concentration factors, defined as the ratio of trace metal concentration in the organism to that in water, give no indication of relative availability among various aquatic systems if the concentration of a trace metal in fish is regulated and independent of concentrations in water. Whole body concentrations of Cu, Mn, and Zn in resident fishes from Skinface Pond were therefore compared with values reported for the same species in other aquatic systems. Similarity of concentrations of a trace metal between differing aquatic systems was accepted as evidence of homeostatic regulation of concentrations of that metal by fish, and concentration factors were not used for assessing availability of that metal. Relationships between concentrations of these metals in whole body, axial musculature, and liver and body size of fishes were also examined for evidence of homeostatic regulation during growth (Cross et al. 1973).

Materials and Methods

Skinface Pond (33°14′N, 81°47′W) is located near Jackson, South Carolina, and adjacent to the U.S. Department of Energy's Savannah River Plant. The shallow (maximum depth ≈2.5 m), 2-ha pond receives no direct inputs of either industrial or domestic wastes. Water in the pond is darkly stained with organic acids during most of the year. The watershed draining into the pond has an estimated area of 14 km² and is managed by the U.S. Forest Service. Upland areas contain 25-yr-old stands of loblolly pine (*Pinus taeda*) and lowland areas contain 50-yr-old stands of mixed hardwoods. The watershed has very low relief, and soils are sandy, highly leached ultisols. Additional description of the regional area has been given by Langley and Marter (1973).

Resident fishes from Skinface Pond were collected on May 22, 1975 after drawdown of the pond and application of rotenone. Only fish that were collected immediately after surfacing were used for trace metal analysis. Fish were transported to the laboratory in ice-filled chests, placed in polyethylene bags, and stored at −4°C until lyophilization. The pond was treated with rotenone again on October 2, 1975 to remove fish that had invaded the pond since the first treatment. None of the fish from the second rotenone treatment was analyzed for trace metals. Replacement of pond water after drawdown and rotenone treatment had little effect on water quality because the pond had a high flushing rate and was not thermally stratified during late autumn and winter. On November 21, 1975, the pond was stocked with 3200 fingerling bluegill and redear sunfish (*L. microlophus*) obtained from the U.S. Fish and Wildlife Service National Fish Hatchery at Orangeburg, S.C. Samples of hatchery-reared, fingerling bluegill and redear sunfish were saved for trace metal analysis. Samples of stocked bluegill were collected at periodic intervals with seines and fish traps. These fish were transported live to the laboratory in polyethylene bags containing pond water and stored in polyethylene bags at −4°C until lyophilization. Despite intensive collection efforts, too few redear sunfish were obtained for analysis.

Water samples were collected monthly in a nonmetallic Kemmerer water sampler at surface, middepth, and 30 cm above bottom from three stations located at the deep end, center, and shallow back end of the pond. Water samples for trace metal analysis were acidified to 2% of volume with redistilled HNO_3 and stored at 4°C in washed polyethylene bottles until analyzed by flameless atomic absorption spectrophotometry, as described by Briese and Giesy (1975), Giesy and Briese (1977), and Giesy et al. (1978). Total organic carbon in pond water was determined with a Beckman model 915 carbon analyzer. Dissolved oxygen, temperature, specific conductance, redox potential, and pH were determined monthly at several depths at each station with a Hydrolab Surveyor model 6D water quality analyzer. Total alkalinity was determined in the field by titration. Binding capacity of surface water from Skinface Pond were determined for Ca, Cd, Cu, and Pb as described by Giesy et al. (1977).

Liver and axial muscle tissues of fish were dissected with stainless steel implements on a clean polyethylene work surface. Polyethylene gloves were worn during dissection of fish tissues to reduce surface contamination of samples. After dissection, tissue samples were placed in washed and tared plastic vials, weighed, and lyophilized to a constant dry weight. Whole fish were dried, digested, and analyzed by atomic absorption spectrophotometry as described by Giesy and Wiener (1977). Methods for cleaning glassware, porcelain crucibles and polyethylene bottles used for sample digestions and storage have also been described (Giesy and Wiener 1977). Both standard additions and additions of NH_4NO_3 were made during Pb determinations to allow partial elimination of matrix interferences by increasing charring (pyrolysis) temperature (Briese and Giesy 1975). Sample preparation and analytical procedures were evaluated and validated, using U.S. National Bureau of Standards (NBS) bovine liver as a reference material. Our results were within the range of concentrations given by NBS for each metal studied.

Blanks used to assess contamination from reagents and container walls do not allow correction for surface contamination resulting from handling of samples (e.g. dissection). Therefore, an additional, statistical approach was employed for each species, metal, and sample type (whole fish, muscle, and liver) to evaluate sample contamination during handling. For each species and sample type, digested samples were diluted to known volumes. For a given species and sample type, the concentrations (corrected for analytical blanks) of each metal in these solutions should be approximately proportional to the respective biomass:dilution volume ratios, barring surface contamination of the samples. For samples diluted to equal volumes, the corrected concentrations of trace metals in the solution should be proportional to the biomass of sample digested. Hence, for each species and sample type, a simple linear regression of blank-corrected metal concentration against sample biomass (or biomass:dilution volume ratio) should yield a regression equation with a significant, positive slope and an inter-

cept that does not differ significantly from zero. Although concentrations of a given trace metal can be highly variable within a given species and sample type, a positive correlation between solution concentration and sample biomass (or biomass:dilution volume ratio) should be demonstrable across a wide range of sample biomass. Given adequate sample size, lack of a positive regression slope, or occurrence of a significant, nonzero intercept suggests surface contamination during sample handling.

Data analyses were conducted with the Statistical Analysis System (Barr et al. 1976). A Type I error of 5% was used to judge significance of statistical tests. In cases of significant analysis of variance, multiple comparison of means were made with Scheffe's test.

Results and Discussion

Analysis of Pond Water

Skinface Pond underwent marked vertical stratification during spring and summer, and the hypolimnion was anoxic during most of this time. Therefore, only data on water from strata containing sufficient dissolved oxygen for fish life were included in the statistical analysis (for inclusion, dissolved oxygen $\geq$3.98 mg/L, the mean threshold of incipient oxygen response reported for nonsalmonid freshwater fishes by Davis (1975)). Hence, means in Table 1 are estimates of annual averages of the measured parameters in the portion of the water column inhabited by fish. Results show that Skinface Pond is typical of freshwaters of the southeastern coastal plain (Beck et al. 1974). The pond is poorly buffered, acidic, and has very low concentrations of dissolved ions (Table 1). Total organic carbon measured in oxygenated surface water ranged from ~15 mg/L to >30 mg/L, indicating the highly organic nature of the pond. Additional chemical description of surface water from Skinface Pond has been given by Giesy et al. (1977).

TABLE 1. Water chemistry data from Skinface Pond. Statistics for all parameters except binding capacity were calculated from average monthly determinations at surface, middepth, and bottom at three stations on the pond over a 1-yr period. Only data from strata containing sufficient dissolved oxygen for fish life were included in the calculations.

Parameter	Mean	Range	C.V. (%)
Temperature (°C)	19	5–31	50
Dissolved oxygen (mg/L)	6.4	4.6–9.2	20
Total alkalinity (mg $CaCO_3$/L)	2.1	1.4–3.0	29
Specific conductance (micromhos/cm)	39	27–58	30
Redox potential (mv)	460	375–525	12
pH	4.6	4.2–5.0	6
Metal concentrations (μg/L)[a]			
Cd	0.17	0.02–0.41	60
Cu	7.6	1.0–15.4	70
Mn	91	39–151	37
Pb	14.1	1.3–34.2	69
Binding capacity (μg-atoms/L)[b]			
Ca	14.3	—	—
Cd	5.2	—	—
Cu	15.0	—	—
Pb	21.0	—	—

[a]Unfiltered water samples.
[b]Pond water with particulates (>0.15 μm) removed.

Evaluation of Contamination of Fish Samples

Blanks used to assess contamination from reagents and container walls indicated substantial sample contamination with Cd but not with Cu, Mn, Pb, or Zn. This applied to all sample collections of resident fishes (from rotenone treatment) and of two sample collections of whole, stocked bluegill. Cadmium concentrations are therefore not reported for these samples. Later investigation showed that Cd contamination occurred during digestion of samples through leaching of Cd from pyrex watch glasses under conditions of high temperature and strong acid.

Linear regression of blank-corrected solution concentration against sample biomass or sample biomass:dilution volume ratio indicated surface contamination of liver and axial muscle samples, though not of whole fish, with Pb. The regression technique indicated no contamination of whole fish or fish tissues by Cu, Mn, or Zn and no surface contamination of whole fish or muscle tissue by Cd in those samples not contaminated with Cd during digestion. Typical regressions are shown for resident warmouth (*L. gulosus*) in Fig. 1. Surface contamination of axial muscle and liver tissues by Pb probably occurred during dissection, due to contact of samples with mucosal surface slime, which contains high concentrations of Pb relative to muscle

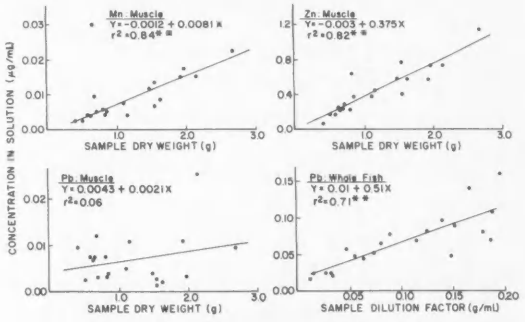

FIG. 1. Checks for surface contamination of fish samples, exemplified for resident warmouth (*Lepomis gulosus*) from Skinface Pond. Surface contamination by Pb is indicated for muscle but not for whole fish samples, whereas no contamination of muscle samples by Mn or Zn is evident (see text). Two asterisks (**) indicate a regression slope that differs from zero at the 1% level of significance. None of the intercepts differ significantly from zero.

TABLE 2. Mean whole body concentrations of Cu, Mn, Pb, and Zn in seven species of resident fishes from Skinface Pond. Concentration ranges are given in parentheses under each mean. Means for a given element that do not contain the same letter in their superscripts were judged significantly different ($\alpha = 0.05$). *Values can be changed to wet weight concentrations by multiplying by 0.25, the mean dry wt:wet wt ratio for whole fish.

Species	n	Dry wt range of fish (g)	Concn (μg/g dry wt)*			
			Cu	Mn	Pb	Zn
Bluegill	17	0.11–82.31	2.15^{a} (1.14–5.91)	40.4^{ab} (14.7–90.7)	1.1^{a} (0.3–4.3)	142^{bc} (56–582)
Warmouth	21	0.62–75.98	2.04^{a} (1.04–3.70)	12.8^{b} (7.5–21.3)	0.8^{abc} (0.3–1.6)	103^{cd} (71–183)
Largemouth bass	22	1.34–277.45	1.88^{a} (1.06–5.30)	4.5^{b} (2.3–19.0)	0.5^{bc} (0.1–1.7)	75^{d} (42–181)
Chain pickerel	20	0.43–150.26	1.60^{a} (1.14–4.19)	14.6^{b} (6.6–58.3)	0.3^{c} (0.05–1.4)	209^{ab} (138–310)
Redfin pickerel	16	0.35–26.04	2.77^{a} (1.18–6.57)	19.3^{b} (5.4–59.0)	1.1^{ab} (0.2–3.0)	216^{a} (126–296)
American eel	13	0.98–88.21	2.34^{a} (1.30–6.43)	9.7^{b} (5.0–16.0)	0.4^{bc} (0.2–1.2)	75^{cd} (61–89)
Lake chubsucker	18	16.83–113.79	2.64^{a} (1.67–3.80)	75.1^{a} (24.0–342.0)	0.4^{c} (0.2–0.6)	79^{cd} (54–102)

and liver (Patterson and Settle 1977). Concentrations of Pb in axial muscle and liver tissue are consequently not presented. A detailed description of precautions for reducing sample contamination by Pb during collection, handling, and analysis has since been published by Patterson and Settle (1976).

TRACE METAL CONCENTRATIONS IN RESIDENT FISHES

Whole body concentrations of Cu, Mn, Pb, and Zn were determined for samples of seven of the more abundant species of fish from the pond, bluegill, warmouth, largemouth bass (*Micropterus salmoides*), chain pickerel (*Esox niger*), redfin pickerel (*Esox americanus americanus*), American eel (*Anguilla rostrata*), and lake chubsucker (*Erimyzon sucetta*) (Table 2). A one-way analysis of variance (ANOVA) indicated significant species effects on whole body concentrations of all four metals. Results of analysis of covariance, with total length as a covariate, were similar. Total length was a significant covariate for Cu, Pb, and Zn and species effects were highly significant ($P < 0.01$) for all four metals after adjusting for length. Copper exhibited less variation among species means than the other metals. Although ANOVA indicated significant species effects on the whole body concentrations of Cu, no two species' means differed significantly, due to the conservative nature of Scheffe's test (Kirk 1968, p. 95).

Mean whole body concentrations of Cu, Mn, and Zn in fish from Skinface Pond were generally similar to the limited data reported elsewhere for samples of the same species collected from relatively uncontaminated systems, suggesting homeostatic regulation of these metals in the whole body. Mean concentrations of Mn and Zn in largemouth bass from five diverse freshwater systems in the southeastern U.S. (Goodyear and Boyd 1972) are approximately equal to mean concentrations given here for that species. However, the mean Cu concentration reported by Goodyear and Boyd (1972) for the five localities (grand mean = 6.2 μg/g) is much higher than that reported here. The mean Cu (2.19 μg/g) and Zn (173 μg/g) concentrations in bluegill from nearby Par Pond (Giesy and Wiener 1977) are very close to those given here for bluegill from Skinface Pond. Mean whole body concentrations of Zn in bluegill (139 μg/g), warmouth (127 μg/g), and largemouth bass (79 μg/g) collected from the uncontaminated portion of a hardwater lake in Indiana (Murphy et al. 1978) were also similar to values given here for those species.

Mean Cu, Mn, and Zn concentrations were lower in axial muscle tissue than in liver tissue in bluegill, largemouth bass, chain pickerel, and bowfin (*Amia calva*) (Table 3). A one-way ANOVA indicated highly significant species effects on concentrations of all three metals for both liver and muscle tissue. Differences in mean concentrations among species were much less pronounced in muscle tissue than in liver tissue. Concentrations in axial muscle tissue were not correlated with concentrations in liver tissue for Cu, Mn, or Zn in either largemouth bass or chain pickerel. A positive correlation should have occurred if these metals were accumulating in the two tissues. Similarly, Pentreath (1976) found no correlation of concentrations of Fe, Mn, or Zn among muscle, liver, and bone tissues of European plaice (*Pleuronectes platessa*).

No species exhibited consistently higher or lower

TABLE 3. Mean concentrations of Cu, Mn, and Zn in axial muscle and liver tissue of resident fishes from Skinface Pond. Concentration ranges are provided in parentheses under each mean. Means for a given element and tissue that do not contain the same letter in their superscripts were judged significantly different ($\alpha = 0.05$). *Values can be changed to wet weight concentrations by multiplying by 0.20 and 0.24, respectively, for axial muscle and liver tissue.

Sample/species	n	Live wt range of fish (g)	Concn (μg/g dry wt)*		
			Cu	Mn	Zn
Axial muscle					
Bluegill	12	97.7–351.2	0.62^{ab} (0.35–1.12)	0.42^{b} (0.23–0.70)	31.7^{a} (12.3–48.7)
Warmouth	20	15.7–236.4	0.61^{b} (0.26–1.99)	0.45^{b} (0.18–2.33)	18.4^{b} (9.0–37.3)
Largemouth bass	19	51.3–1191.8	1.08^{a} (0.46–2.52)	0.32^{b} (0.13–0.59)	12.7^{b} (7.0–24.5)
Chain pickerel	16	94.9–773.7	0.29^{b} (0.06–0.88)	1.21^{a} (0.19–2.30)	14.7^{b} (4.9–32.8)
Bowfin	4	1192–2561	0.85^{ab} (0.49–1.48)	0.87^{ab} (0.65–1.40)	22.2^{ab} (18.0–26.3)
Liver					
Bluegill	4	192.5–285.8	4.8^{b} (4.1–5.6)	7.18^{a} (2.58–12.96)	39.7^{b} (21.3–55.4)
Largemouth bass	17	178.5–1191.8	24.8^{b} (6.7–105.8)	3.69^{b} (2.24–5.55)	74.4^{b} (18.9–173.9)
Chain pickerel	13	94.9–396.5	27.8^{b} (10.2–54.4)	1.77^{c} (0.80–2.68)	337.9^{a} (150.0–855.6)
Bowfin	4	1192–2561	548.1^{a} (250.8–918.9)	4.97^{ab} (2.99–7.05)	85.7^{b} (45.7–121.3)

concentrations of Cu, Mn, and Zn in either whole body, axial musculature, or liver tissue, and no trophic level biomagnification of Cu, Mn, Pb, and Zn was observed among fishes of different trophic position. Species differences in trace metal concentrations of fish tissues and/or whole fish from a single locality have been reported elsewhere (Lucas et al. 1970; Cross and Brooks 1973; Lentsch et al. 1973; Ting 1973; Gilmartin and Revelante 1975; Hutchinson et al. 1976; Giesy and Wiener 1977; Murphy et al. 1978). Except for Hg (Leland et al. 1977), there has been essentially no indication of higher concentrations of trace metals in fishes of higher trophic status relative to fishes of lower trophic status (Mathis and Cummings 1973; Ting 1973; Stevens and Brown 1974; Hutchinson et al. 1976; Giesy and Wiener 1977; Murphy et al. 1978). In addition, fishes having similar food habits may exhibit marked differences in whole body (Cross and Brooks 1973) or tissue concentrations (Ting 1973) of certain trace metals. Adult chain pickerel and largemouth bass are primarily piscivorous; however, mean trace metal concentrations for these species in Skinface Pond often differed significantly (Tables 2 and 3). Trace metal concentrations in fish are apparently related to factors other than food habits and trophic status.

Results of correlational analyses between body size and Cu, Mn, and Zn concentrations provided further empirical evidence of homeostatic regulation of these metals in fish. We found negative correlations between whole body concentrations of Cu, Mn, and Zn and total length for all species analyzed except lake chubsucker (Table 4). Decreases in whole body concentrations of essential trace metals with increasing body size of fish have been reported elsewhere (Cross and Brooks 1973; Bohn and McElroy 1976; Giesy and Wiener 1977; Murphy et al. 1978). However, increasing whole body concentrations of Zn with body size of fish have also been observed (Bohn and McElroy 1976; Cutshall et al. 1977). Cross and Brooks (1973) suggested that decreases in whole body concentrations with size result from shifts in the relative proportions of body tissues that have differing metal concentrations.

Copper, Mn, and Zn concentrations in liver and axial muscle tissue were generally not correlated with body size of fish from Skinface Pond (Table 4), similar to results reported elsewhere (Cross et al. 1973; Eustace 1974; Mathis and Kevern 1975; Pentreath 1976; Bohn and McElroy 1976).

TRACE METAL CONCENTRATIONS IN STOCKED BLUEGILL

A one-way ANOVA indicated highly significant temporal changes in whole body concentrations of Cu, Pb, and Zn in bluegill that were stocked into Skinface Pond, but no trend of increasing concentrations with time was apparent (Table 5). Mean whole body con-

TABLE 4. Correlation coefficients (r) between total length and dry weight concentrations of trace metals in whole body, axial muscle tissue, and liver tissue of resident fishes from Skinface Pond. Only significant correlation coefficients ($\alpha = 0.05$) are given. Nonsignificant correlations are indicated by ns; *r significant at the 5% level; **r significant at the 1% level.

Sample and species analyzed	n	Cu	Mn	Pb	Zn
Whole body					
Bluegill	17	−0.68**	ns	−0.48*	−0.79**
Warmouth	21	−0.68**	ns	−0.66**	−0.84**
Largemouth bass	22	−0.72**	−0.63**	−0.53*	−0.84**
Chain pickerel	20	−0.70**	−0.61**	−0.56*	ns
Redfin pickerel	16	ns	−0.60*	ns	−0.79**
American eel	13	−0.89**	ns	−0.91**	ns
Lake chubsucker	18	ns	ns	ns	ns
Muscle					
Bluegill	12	ns	ns	—	ns
Warmouth	20	ns	ns	—	ns
Largemouth bass	19	ns	−0.48*	—	ns
Chain pickerel	16	ns	ns	—	ns
Liver					
Largemouth bass	17	ns	ns	—	0.60*
Chain pickerel	13	ns	ns	—	ns

centrations of Zn in bluegill decreased and remained constant at approximately 100 μg/g dry wt as of 220 d after stocking. Whole body concentrations of Cu and Pb were highest in fingerling bluegill collected 97 d after stocking and decreased to relatively constant levels in samples collected during and after 220 d. Cadmium and Mn concentrations were relatively constant in whole bluegill throughout the collection period.

One-way ANOVA indicated highly significant temporal variation in Mn and Zn concentrations in axial muscle tissue of bluegill collected 216, 360, and 511 d after stocking (Table 6). Residence time of stocked bluegill in the pond did not significantly affect Cd or Cu concentrations in axial muscle tissue. Hence, there was no general trend of increasing concentrations of the four metals in muscle tissue with time.

Whole body Cu and Zn concentrations were higher ($P < 0.01$, t-test) whereas Mn and Pb concentrations were lower ($P < 0.05$ for Pb, $P < 0.01$ for Mn) in stocked bluegill recaptured after 499 d than in larger (dry wt > 5 g, $n = 12$) resident bluegill collected during rotenone treatment. Only mean whole body concentrations of Mn differed between resident and stocked bluegill by a factor of more than 2. In contrast to whole body concentrations, mean Cu, Mn, and Zn concentrations in muscle tissue of resident (Table 3) and stocked bluegill (Table 6, time = 511 d) were similar and differed significantly only for Mn (t-test, $P < 0.01$). How-

TABLE 5. Mean whole body concentrations of trace metals in bluegill collected during and after stocking of Skinface Pond. Concentration ranges are provided in parentheses under each mean. Means for Cu, Pb, or Zn that do not contain the same letter in their superscripts were judged significantly different ($\alpha = 0.05$).

Time (days after stocking)	n	Dry wt range (g)	Concn (μg/g dry wt)				
			Cd	Cu	Mn	Pb	Zn
0	12	0.02–0.41	0.07 (0.02–0.23)	11.5[b] (2.8–63.3)	21.4 (14.4–44.8)	0.19[b] (0.00–0.76)	349[a] (177–660)
97	12	0.04–0.27	0.07 (0.04–0.12)	324.9[a] (247.6–404.0)	20.7 (15.1–29.8)	1.22[a] (0.43–5.49)	249[b] (153–365)
220	15	3.64–13.97	—	2.5[b] (0.9–4.4)	16.0 (8.9–18.9)	0.29[b] (0.04–0.63)	106[c] (95–124)
340	11	3.97–15.13	—	1.7[b] (1.2–2.1)	18.2 (10.0–26.5)	0.14[b] (0.04–0.30)	100[c] (84–120)
499	10	6.6–23.8	0.04 (0.01–0.09)	2.8[b] (1.6–3.9)	19.9 (14.2–25.7)	0.47[ab] (0.12–0.76)	102[c] (85–117)

TABLE 6. Mean dry weight concentrations of trace metals in muscle tissue of bluegill collected after stocking of Skinface Pond. Concentration ranges are provided in parentheses under each mean. Means for Mn or Zn that do not contain the same letter in their superscripts were judged significantly different ($\alpha = 0.05$).

Time (days after stocking)	n	Live wt range of fish (g)	Concn (μg/g dry wt)			
			Cd	Cu	Mn	Zn
216	13	29.6–57.1	0.0092 (0.0029–0.0361)	1.28 (0.46–5.78)	0.38[a] (0.18–0.58)	41.4[a] (31.5–57.4)
360	11	43.6–82.2	0.0040 (0.0008–0.0108)	0.52 (0.40–0.69)	0.39[a] (0.26–0.59)	34.8[b] (28.1–42.6)
511	11	61.3–124.9	0.0088 (0.0037–0.0164)	0.51 (0.38–0.66)	0.75[b] (0.60–0.95)	31.3[b] (24.6–38.2)

ever, the mean concentration of Mn in muscle tissue of resident bluegill was similar to those in stocked bluegill collected 216 and 360 d after release. Although whole body concentrations of Cu, Mn, and Zn differed between resident and stocked bluegill, average concentrations of these metals in muscle tissue from the two populations were similar. Concentrations of these trace metals in muscle tissue were apparently regulated. Concentrations of Cd, Cu, Mn, Pb (calculated without correcting for surface contamination), and Zn in muscle tissue were low, indicating that only small quantities of these metals were accumulated there.

Availability of Cd and Pb in Skinface Pond to stocked bluegill was compared with availability in hardwater systems with concentration factors (Jinks and Eisenbud 1972). Concentration factors (CF) between water and stocked bluegill were calculated with the formula

$$CF = \frac{C_o}{C_w}$$

where C_o = dry weight concentration of a given trace metal in the organism (bluegill), and

C_w = average total concentration of the trace metal in water. Annual average concentrations of metals in water (Table 1) were used for C_w for Skinface Pond, as suggested by Lentsch et al. (1973). In addition, C_w were determined from unfiltered water samples, as suggested by Vanderploeg et al. (1975). *CF* were determined for whole bluegill collected approximately 500 d after stocking (Table 7). These CF may be considered equilibrium values because metal concentrations in whole bluegill were relatively stable by approximately 200 d after stocking (Table 5). Because concentrations of trace metals other than Hg are strongly regulated in axial muscle tissue of fish (Phillips 1977), *CF* were not calculated for muscle tissue. *CF* for Cu and Mn in Table 7 were not used for comparative purposes because of homeostatic regulation. For comparison, *CF* for Cd and Pb were calculated for whole bluegill from three hardwater systems (total alkalinity >100 mg/L $CaCO_3$) in Indiana (Palestine Lake: ditch; Palestine Lake: east basin; and Little Center Lake) with data published by Atchison et al. (1977). Mean whole body concentrations for bluegill and estimated mean total concentrations in water (total = mean dissolved concentration + mean suspended concentration) were used in the calculations.

The slight differences in body size distributions between the samples of bluegill from Indiana Lakes and Skinface Pond should not affect our comparison of availability. Whole body concentrations of Cd were not correlated with body size in bluegill from either Palestine Lake (Murphy et al. 1978) or Skinface Pond (Table 5). Differences in the size distributions between samples of bluegill from Little Center Lake and Skinface Pond were small. Total length median and range for the sample from Little Center Lake were 115 and 81–177 mm, respectively, whereas median and range for the Skinface Pond sample were 154 and 118–163 mm, respectively. In addition, the relationship between Pb concentration and total length accounted for only 23% of the variation in Pb concentration in whole, resident bluegill from Skinface Pond (Table 4).

CF for Cd for the three Indiana sites were lower than the *CF* for whole bluegill from Skinface Pond (Table 7). In contrast, the *CF* for Pb in bluegill from Little Center Lake was much higher than for bluegill from Skinface Pond. Lead concentrations in water and bluegill from the other two sites in Indiana were below the detection limits of the methods employed by Atchison et al. (1977).

TABLE 7. Concentration factors (*CF*) for whole bluegill collected from Skinface Pond approximately 500 d after stocking, relative to *CF* for bluegill collected from hardwater lakes in Indiana by Atchison et al. (1977) (see text).

Element	*CF*	
	Skinface Pond	Hardwater Lakes
Cd	240	71[a], 83[b], 120[c]
Cu	370	—
Mn	220	—
Pb	33	230[c]

[a]Palestine Lake: ditch.
[b]Palestine Lake: east basin.
[c]Little Center Lake.

We assume that a greater *CF* for a metal indicates greater availability of that metal in the environment. The *CF* for Cd in Skinface Pond is approximately 2.6 times greater than the mean *CF* for Cd in the hardwater systems studied by Atchison et al. (1977). Although the statistical significance of this difference cannot be assessed, we believe that Cd in Skinface Pond is possibly more available, but at least as available to fish as in hardwater lakes. Proportionately more Cd may exist as the free divalent cation in acidic, highly organic waters than in hardwater systems because controls on Cd^{2+} concentration in surface waters are primarily inorganic, and very little Cd is bound to either organic or inorganic ligands in waters having low pH and high organic carbon concentration (Giesy et al. 1978). This may explain the greater availability of Cd in Skinface Pond, relative to hardwater lakes. In contrast, Pb in Skinface Pond was relatively unavailable to fish. A lower *CF* for Pb in a highly organic system is not surprising. The binding capacity of Skinface Pond water for Pb was about 4 times greater than that for Cd (Table 1). Most of the Pb in these waters is associated with high molecular weight organic acids and particulate matter (Giesy and Briese 1977) and is not in the ionic form (Pb^{2+}), which is readily available for direct uptake through the gills of fish (Holcombe et al. 1976; Merlini and Pozzi 1977a, b). Although it is unclear whether uptake from water or food accounts for the majority of Pb accumulation in fish inhabiting natural systems, Pb is less available to fish in Skinface Pond than in hardwater lakes. Because fish readily accumulate available (ionic) Pb (Holcombe et al. 1976; Merlini and Pozzi 1977a, b), we believe the negative correlations between whole body concentrations of Pb and body size in resident fishes (Table 4) further indicate low availability of Pb in Skinface Pond to fish.

In a recent review, Jenne and Luoma (1977) suggested that biotic accumulation of trace elements present at similar total concentrations would vary inversely with concentrations of dissolved organics. Although our findings for Pb support their suggestion, our findings for Cd indicate that it should not be generally applied to all trace metals and all waters. We stress the need for metal-specific analysis of biological availability of metals in highly organic, softwater systems.

Much of the information presented here indicates homeostatic regulation of Cu, Mn, and Zn in resident and stocked fish from Skinface Pond. Despite considerable differences in ambient metal concentrations and other chemical characteristics, mean whole body concentrations of Cu, Mn, and Zn in resident fishes from Skinface Pond were generally similar to values reported elsewhere for the same species and remained constant or decreased slightly with increasing body size. Also, Cu, Mn, and Zn concentrations did not vary with body size in liver tissue or axial musculature. Similarly, mean axial muscle and whole body concentrations of Cu, Mn, and Zn in stocked bluegill were relatively constant approximately 200 d after stocking and did not change substantially with growth. Hence, these metals did not accumulate in the tissues with age. Further evidence of homeostatic regulation of Cu, Mn, and Zn has been presented by Schroeder et al. (1966), Goodyear and Boyd (1972), Cross et al. (1973), Lentsch et al. (1973), Merlini et al. (1973), and Giesy and Wiener (1977).

These results have important implications for biological monitoring programs. An organism or group of organisms is of no value for biological monitoring of a trace metal if concentration of that metal in the organism is regulated and independent of ambient concentrations. Use of fish for such monitoring should therefore be limited to nonessential metals that accumulate in the body with exposure.

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Comparative Susceptibility of Atlantic (*Salmo salar*) and Coho (*Oncorhynchus kisutch*) Salmon to Three Strains of *Vibrio anguillarum* from the Maine–New Hampshire Coast[1]

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SAWYER, E. S., R. G. STROUT, AND B. A. COUTERMARSH. 1979. Comparative susceptibility of Atlantic (*Salmo salar*) and coho (*Oncorhynchus kisutch*) salmon to three strains of *Vibrio anguillarum* from the Maine–New Hampshire coast. J. Fish. Res. Board Can. 36: 280–282.

Atlantic salmon (*Salmo salar*) were found to be as susceptible as coho salmon (*Oncorhynchus kisutch*) to Maine–New Hampshire strains of *Vibrio anguillarum* used in both injection and water transmission exposure. Exposure to 1–2.5 × 10^5 organisms/mL of one strain (569) in the water for 1 h killed 80–100% of Atlantic salmon at 10 and 15°C. Should similar water exposure conditions occur in Maine estuaries, newly released Atlantic salmon smolts may encounter lethal levels of *V. anguillarum*.

Key words: Vibrio anguillarum, *Salmo salar*, Atlantic salmon, susceptibility, marine bacteria.

SAWYER, E. S., R. G. STROUT, AND B. A. COUTERMARSH. 1979. Comparative susceptibility of Atlantic (*Salmo salar*) and coho (*Oncorhynchus kisutch*) salmon to three strains of *Vibrio anguillarum* from the Maine–New Hampshire coast. J. Fish. Res. Board Can. 36: 280–282.

Nous constatons que le saumon atlantique (*Salmo salar*) est aussi susceptible que le saumon coho (*Oncorhynchus kisutch*) aux souches Maine–New Hampshire de *Vibrio anguillarum*, tant à la suite d'une injection que par transmission dans l'eau. L'exposition à une concentration de 1 à 2,5 × 10^5 organismes/L d'une souche (569) dans l'eau pendant 1 h tue de 80 à 100% des saumons atlantiques à 10°C et à 15°C. S'il existait de semblables conditions dans les estuaires du Maine, les smolts de saumon atlantique nouvellement mis en liberté pourraient être exposés à des niveaux létaux de *V. anguillarum*.

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Vibrio anguillarum, a marine bacterium, has caused high mortality among cultured and wild salmonids in North America, Europe, and Japan (Egidius and Andersen 1977; Fryer et al. 1972; Haastein and Holt 1972). Vibriosis has been a major problem for salmonid mariculturists in Maine and New Hampshire where we found a serological heterogeneity in *V. anguillarum* isolated from pen-reared coho salmon (*Oncorhynchus kisutch*), and rainbow trout (*Salmo gairdneri*), and from nonsalmonid feral fishes (Strout et al. 1978).

Currently, the Maine Sea-Run Atlantic Salmon Commission, in cooperation with the U.S. Fish and Wildlife Service, releases several hundred thousand Atlantic salmon (*Salmo salar*) smolts each spring into Maine estuaries where *V. anguillarum* has been found in other species. Although there have been no reports of vibriosis in these salmon, they are almost certainly exposed to the disease. Garrison (1973) reported that Atlantic salmon were susceptible to Pacific Coast strains of *V. anguillarum* and that some immunity could be produced by an oral bacterin. A vibriosis bacterin from Maine–New Hampshire strains of *Vibrio* has been effective in preventing or reducing mortality in local pen-reared coho salmon (Sawyer and Strout 1977) and might also be effective for Maine stocks of Atlantic salmon should they prove equally susceptible. Therefore, our purpose was to compare susceptibility of Atlantic and coho salmon to *V. anguillarum* infections.

Materials and methods — We used three antigenically different strains (775A, 569, and 507) as representative of three serotypes of *V. anguillarum* found locally (Strout et al. 1978). These strains were typical of those found in

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TABLE 1. Susceptibility of Atlantic (*Salmo salar*) and coho (*Oncorhynchus kisutch*) salmon to injection of three strains of Maine–New Hampshire *Vibrio anguillarum*.

	Atlantic salmon						Coho salmon					
	10°C			15°C			10°C			15°C		
Strain and no. organisms injected	Mortality (%)		Time until death (h)[a]	Mortality (%)		Time until death (h)	Mortality (%)		Time until death (h)	Mortality (%)		Time until death (h)
	Trial 1	Trial 2		Trial 1	Trial 2		Trial 1	Trial 2		Trial 1	Trial 2	
775A												
$1–2.5\times10^7$	40	100	24–96	60	100	12–96	100	100	48–96	100	100	24–72
$1–2.5\times10^3$	0	0	—	0	0	—	0	0	—	0	0	—
569												
$1–2.5\times10^7$	100	100	6–24	100	100	6–12	100	100	12–24	100	100	3–12
$1–2.5\times10^3$	0	100	48–72	100	100	48–96	0	20	–96	20	100	96–120
507												
$1–2.5\times10^7$	100	100	48–96	0	100	24–48	0	40	72–96	100	100	12–24
$1–2.5\times10^3$	0	40	72–96	0	100	48–72	0	0		80	100	72–96

[a]Minimum and maximum for duplicate trials.

cultured and feral fishes from estuaries of the Piscataqua, Saco, Sheepscot, and Penobscot rivers. Atlantic salmon smolts were obtained from the Craig Brook National Fish Hatchery in East Orland, Maine; coho salmon were from the University of New Hampshire Sea Grant Hatchery at Newmarket, New Hampshire.

Experiments were run in duplicate and involved several dose levels, two temperatures (10 and 15°C), and two methods of exposing the fish (individual injection and water transmission) to live *V. anguillarum*. The injection method was used as a measure of virulence, and the water exposure method as a measure of both virulence and invasiveness.

Injection — Cultures of three strains of *V. anguillarum* (775A, 569, and 507), grown in Trypticase® Soy Agar plus 1% NaCl at 20°C for 24 h were suspended in sterile saline and diluted to doses of approx. $1–2.5 \times 10^8$ cells/mL or $1–2.5 \times 10^4$ cells/mL. In each of the duplicate trials, six groups of five Atlantic salmon averaging 30 g each were held in 38-L aquaria with filters and airstones. Each group of salmon received one of the three strains of live *V. anguillarum* at either a high or low dose. Individual fish were injected in the dorsal sinus (immediately posterior to the dorsal fin) with 0.1 mL of the designated strain and dosage. Controls were injected with saline only. Time until death was recorded and all dead fish were examined bacteriologically. Biochemical tests and slide agglutination tests with specific rabbit antisera were used to identify all isolates. The experiment was repeated with coho salmon averaging 38 g each.

Water transmission — We attempted to infect both Atlantic and coho salmon by exposing them to known numbers of *V. anguillarum* in the water. Only strain 569 was used in the water transmission tests because it was representative of our most widespread serotype and also proved to be the most virulent in the injection tests. In each of the duplicate trials six groups of five 30-g Atlantic salmon were exposed to live *V. anguillarum* by placing the fish in 2 L of artificial seawater (15‰) containing $1–2.5 \times 10^7$, 10^5, or 10^3 cells/mL for 30 min or 1 h. Fish were then returned to aquaria containing clean freshwater. Controls were exposed to 15‰ artificial seawater for 30 min or 1 h and then returned to freshwater. The experiment was repeated with coho salmon averaging 40 g.

Results — The mortality pattern resulting from *V. anguillarum* was similar for both coho and Atlantic salmon with regard to dose, temperature, route of exposure, and time until death (Table 1 and 2). The disagreement in results between duplicate trials may be explained by the 120-h observation period. In recent experiments we found that mortality continues for up to 2 wk after exposure. As expected, an increase in exposure time, numbers of *V. anguillarum*, or temperature produced higher mortality and shorter time to death. *Vibrio anguillarum* was recovered from the kidneys of all but two dead fish. There was no mortality in control fish at either temperature or method of exposure.

Discussion — The two results most relevant to field situations are (1) the overall similarities in susceptibility of the two salmonid species, and (2) the water transmission exposure level that consistently killed Atlantic salmon.

Laboratory exposures of $1–2.5 \times 10^5$ cells/mL in water of *V. anguillarum* (strain 569) for 1 h at either 10 or 15°C killed 80–100% of the Atlantic salmon. These temperatures are typical of those in the estuaries when Atlantic salmon are released; the natural exposure time as shown by tracking studies for newly released smolts is 1–2 d (Fried 1977). The numbers of *V. anguillarum* in Maine estuaries at these temperatures have not been investigated, but the work of Murchelano et al. (1975)

TABLE 2. Susceptibility of Atlantic (*Salmo salar*) and coho (*Oncorhynchus kisutch*) salmon to water transmission of a Maine–New Hampshire strain of *Vibrio anguillarum*.

No. organisms/mL and exposure time	Atlantic salmon						Coho salmon					
	10°C			15°C			10°C			15°C		
	Mortality (%)		Time until death (h)[a]	Mortality (%)		Time until death (h)	Mortality (%)		Time until death (h)	Mortality (%)		Time until death (h)
	Trial 1	Trial 2		Trial 1	Trial 2		Trial 1	Trial 2		Trial 1	Trial 2	
$1–2.5\times10^{7}$ (30 min)	100	100	24–72	100	100	4–36	100	100	24–96	100	80	12–48
$1–2.5\times10^{5}$ (1 h)	100	80	96–120	80	100	72–120	40	20	96–120	100	40	48–72
$1–2.5\times10^{6}$ (30 min)	0	0	—	0	40	96–120	0	0	—	0	0	—
$1–2.5\times10^{3}$ (1 h)	0	0	—	0	0	—	0	0	—	0	0	—

[a]Minimum and maximum for duplicate trials.

in Long Island Sound suggests that a total of 10^5 organisms/mL is possible in some areas. It is also possible that fewer *V. anguillarum* would be required to produce the disease on a prolonged exposure of 1–2 d or more.

Considering the relatively short observation time and small numbers of fish held under laboratory conditions, it appears that susceptibility of Atlantic and coho salmon to Maine–New Hampshire strains of *V. anguillarum* is similar. Immunization of Atlantic salmon smolts with local strains of *V. anguillarum* might significantly improve the percentage returns of this speices.

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Iodine Balance in Rainbow Trout (*Salmo gairdneri*) and Effects of Testosterone Propionate

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HUNT, D. W. C., AND J. G. EALES. 1979. Iodine balance in rainbow trout (*Salmo gairdneri*) and effects of testosterone propionate. J. Fish. Res. Board Can. 36: 282–285.

Iodine balance was studied in immature rainbow trout (*Salmo gairdneri*) held at 12°C in water of iodine content 1.85 μg/L and fed daily 1% of body weight with food containing 0.48 μg I/g. Iodide flux into the plasma pool was 148 ng $I \cdot h^{-1} \cdot 100\ g^{-1}$ of which <1% was contributed by peripheral deiodination of thyroid hormones, up to 16% was obtained from the diet,

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and at least 84% was derived from the water. Less than 5% of iodide intake was required to satisfy thyroidal secretory demands. Testosterone injections elevated plasma iodide and protein levels, but did not alter the rate of plasma iodide turnover.

Key words: trout, iodine balance, thyroid function, testosterone

HUNT, D. W. C., AND J. G. EALES. 1979. Iodine balance in rainbow trout (*Salmo gairdneri*) and effects of testosterone propionate. J. Fish. Res. Board Can. 36: 282–285.

Nous avons étudié le bilan de l'iode dans des truites arc-en-ciel (*Salmo gairdneri*) maintenues à 12°C dans de l'eau dont la teneur en iode était de 1,85 μg/L et auxquelles on avait donné quotidiennement 1% de leur poids corporel en nourriture contenant 0,48 μg I/g. Le flux de l'iode dans la masse plasmatique est de 148 ngI·h^{-1}·100 g^{-1}, dont moins de 1% provenait d'une désiodisation périphérique des hormones thyroïdinnes, jusqu'à 16% du régime alimentaire et au moins 84% de l'eau. Moins de 5% de la quantité d'iode absorbée est requis pour satisfaire aux demandes de la secrétion thyroïdienne. Des injections de testostérone élèvent les niveaux de l'iode et des protéines plasmatiques, mais ne modifient pas la vitesse de renouvellement de l'iode plasmatique.

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UNDER certain conditions iodine intake may be inadequate to support normal thyroid function in freshwater teleosts (Marine and Lenhart 1911; Hoar and Bell 1950; Hoar 1952; Baker-Cohen 1959; Radulescu et al. 1968; Black and Simpson 1974; Drongowski et al. 1975; Sonstegard and Leatherland 1976). It is therefore surprising that despite several studies on dietary iodine requirements (Woodall and LaRoche 1964; La Roche et al. 1965) and radioiodide kinetics (Hickman 1959, 1962; Leloup and Fontaine 1960; Hunn and Reineke 1964; Leloup 1970; Gregory and Eales 1974), no comprehensive study of iodine balance in teleosts has been undertaken. Thus, there are no estimates of (i) rate of iodide entry into, or loss from, the plasma pool, (ii) relative contributions of dietary iodide, ambient iodide, or iodide derived from the peripheral deiodination of thyroid hormones to the plasma iodide pool, (iii) the proportion of iodide intake necessary to satisfy thyroidal secretory demands, and (iv) changes in iodide economy during activation of the thyroidal system. In the present study the above parameters have been measured using both control trout and trout in which the thyroidal system was stimulated by testosterone treatment (Hunt and Eales 1979).

Materials and methods — Two-year-old immature rainbow trout (*Salmo gairdneri*) acclimated in running dechlorinated Winnipeg City water (iodine content 1.85 μg/L at 12°C were fed Ewos trout pellets (Astra Chemicals Ltd., Mississauga, Ontario; iodine content 0.52 μg/g dry weight, or 0.48 μg/g wet weight) once each day at a ration of 1% of wet body weight. The photoperiod was 12L:12D.

Two groups of 92 trout ($\bar{x} \pm \text{SE} = 115 \pm 2$ g) were injected intramuscularly every 4th d for a total of five injections with 0 μg (controls) or 30 μg of TP (testosterone propionate) (Sigma) in 20 μL of peanut oil. Four days after the last injection each fish was injected into the coloem with 1.85 GBq of carrier-free $Na^{131}I$ in 20 μL distilled water. Groups of 8–10 fish were bled at intervals ranging from 0.5 to 96 h after injection. Plasma radioiodide was isolated by column separation (Eales 1977), and the percent of the injected $Na^{131}I$ dose present in 1 mL of plasma (normalized to a body weight of 100 g) determined.

The rate of loss of plasma iodide measured as μg I·h^{-1}·100 g^{-1} body weight, was determined by the product of the plasma iodide pool and the fractional rate constant for iodide loss from plasma (k, fraction/h). The plasma iodide pool was obtained from the product of the plasma iodide concentration (μg/mL) and the plasma iodide distribution space (DS). DS was determined as $100/I_0$, where I_0 represents the percent injected $Na^{131}I$ dose present in 1 mL of plasma as $^{131}I^-$ at zero time (Y intercept). k was provided by the slope of the regression relating the natural logarithm of percent dose per millilitre plasma to time (hours). Total levels of ^{127}I in plasma, food, or water were determined by the Hycel method (Higgs and Eales 1971).

The thyroxine (T_4) degradation rate (T_4DR) was determined by following the kinetics of ^{125}I–T_4, which was injected into the heart region at the same time as $Na^{131}I$ was injected into the coloem. The T_4 kinetics have been reported in detail elsewhere (Hunt and Eales 1979) and only the T_4DR values and T_4 deiodination rates obtained from that analysis are referred to here.

Plasma protein was determined by the Biuret method.

Statistical differences between means were determined using Students *t-test*. The regressions describing plasma loss of $^{131}I^-$ with time were compared by analysis of covariance.

Results and discussion — Table 1 indicates that for control trout the plasma iodide pool is 9.9 μg/100 g body weight and is turned over at a rate of 1.5%/h (Fig. 1), resulting in an iodide excretion rate of 148 ng I·h^{-1}·100 g^{-1}.

Table 2 shows estimates of contributions to the plasma iodide pool from deiodination, dietary, and ambient sources. The iodide derived from peripheral deiodination of thyroid hormones was determined directly from the T_4DR (Hunt and Eales 1979) and found to be <1% of the iodide influx. A dietary iodide contribution of 16% was estimated from the iodide food content, assuming that each fish ate its prescribed 1% daily ration of food and that all ingested iodide

TABLE 1. Effect of testosterone propionate on plasma protein levels and various parameters of iodine metabolism in immature rainbow trout. All kinetic parameters normalized to a body weight of 100 g. Numbers in parentheses are 95% confidence intervals of the mean.

Parameter	Control	TP-injected	% change from control
Plasma iodine (^{127}I) μg/mL)	0.82 (±0.23)	1.13 (±0.14)	+38[b]
Iodide distribution space (mL)	12.0 (±0.14)	10.6 (±0.08)	−12
Plasma iodide pool (μg)	9.9	11.9	+20
k (fraction/h)	0.0150	0.0135	−10
Iodide excretion rate (ng/h)	148	162	+9
Hormonal iodine degradation rate (ng/h)[a]	6.3	8.3	+32
Plasma protein (mg/mL)	31.1 (±0.38)	38.1 (±0.24)	+23[b]

[a]Derived from T_4DR (Hunt and Eales 1979).
[b]$P < 0.01$.

was absorbed into the blood. These assumptions are reasonable as all food was eaten and iodide is efficiently absorbed from the trout gut (Gregory and Eales 1974). Iodide intake unaccounted for by deiodination or dietary routes was 83% and presumably represents iodide uptake from the water. Extensive branchial iodide uptake has been claimed in trout (Leloup 1970), although the reported iodide fluxes (7-17 ng $I \cdot h^{-1} \cdot 100\ g^{-1}$) were lower than recorded here (123.6–137 ng $I \cdot h^{-1} \cdot 100\ g^{-1}$). This may reflect a difference in ambient iodide level, since Leloup found that the branchial iodide flux increased with ambient iodide concentration. Extensive branchial iodide uptake was also implied in the study of Higgs and Eales (1971) who found elevated plasma iodide in brook trout starved for several weeks. On the other hand, Gregory and Eales (1974) demonstrated a dependance of plasma iodide on diets containing high iodide levels. It is clear that the relative contributions of dietary and ambient iodide to the plasma iodide pool will depend on the availability of iodide from these two sources.

The quantity of iodine secreted from the thyroid gland as T_4 was determined from T_4DR (Hunt and Eales 1979) and found to be 6.3 ng $\cdot h^{-1} \cdot 100\ g^{-1}$. This represents about 4% of the total plasma iodide pool turned over each hour, indicating that for the rainbow trout held under present laboratory conditions the bulk of the iodide traversing the plasma pool is not destined for thyroidal use.

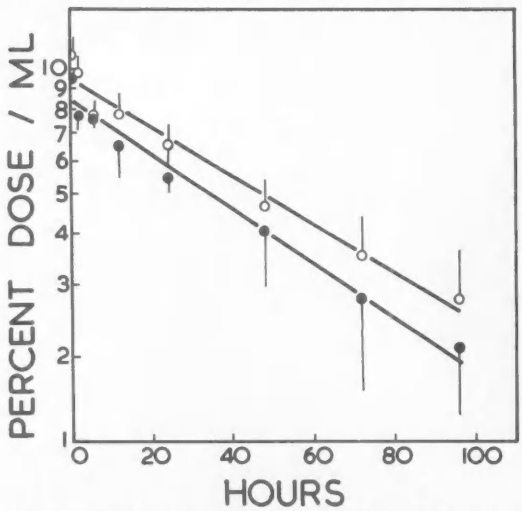

FIG. 1. Relationship between plasma $^{131}I^-$ and the time following intraperitoneal $Na^{131}I$ injection in control (●) and TP-injected trout (○). Regressions were calculated by least squares for samples from 0.5 to 96 h. Geometric means with 95% confidence intervals are presented.

TABLE 2. Estimated contributions of iodide from deiodination, dietary, and ambient sources to the iodide intake into the plasma pool of control and testosterone propionate (TP)-treated rainbow trout.

Iodide source	Control		TP-treated	
	ng $\cdot h^{-1} \cdot 100\ g^{-1}$	%	ng $\cdot h^{-1} \cdot 100\ g^{-1}$	%
Deiodination[a]	0.7	0.5	1.0	0.6
Diet[b]	23.7	16.0	24.0	14.8
Ambient[c]	123.6	83.5	137.0	84.6
Totals	148.0	100.0	162.0	100.0

[a]Iodide contribution to plasma iodide pool from T_4 deiodination was estimated as the product of the hormonal iodine degradation rate (Table 1) and the fraction of the hormonal iodine removed by deiodination. These latter fractions were calculated as 0.40 (control) and 0.51 (TP) (Hunt and Eales 1979). Iodide generation is 25% of this value since only one of the four iodine atoms is liberated from T_4 by deiodination.
[b]Based on the assumption that on the average each fish eats 1% of its body weight of food/day and that all the available iodine is absorbed as iodide into the plasma pool.
[c]Obtained by subtracting the combined iodide intakes from dietary and deiodination sources from the total iodide excretion rate for plasma.

Plasma iodide (^{127}I) was significantly ($P < 0.01$) elevated by 38% due to TP treatment (Table 1). Although heterogeneity of variance precluded comparison of the regressions for plasma $^{131}I^-$ loss (Fig. 1), both the iodide distribution space and k seemed reduced in the TP trout. This resulted in an iodide excretion rate that was only 9% greater for TP trout (Table 1), indicating the danger of evaluating iodide balance in terms of plasma iodide levels alone. The elevation of plasma iodide, as well as the changes in iodide distribution space and k, could be secondary to the significant ($P < 0.01$) 23% increase in plasma protein due to TP treatment. Like other clupeiforms, trout possess an iodide-binding plasma protein (Huang and Hickman 1968; Leloup 1970; Gregory and Eales 1974; Perrier et al. 1976). If this particular protein fraction were increased by TP it would tend to elevate the plasma $^{127}I^-$ level, decrease the iodide distribution space, and decrease the fractional rate of plasma iodide loss. Because testosterone treatment stimulates thyroidal function and increases the T_4DR in trout (Hunt and Eales 1979), the above effects of TP on iodide metabolism could be of advantage under iodide–deficiency conditions.

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Role of Phosphorus in Great Lakes Eutrophication: Is There a Controversy?

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SCHELSKE, C. L. 1979. Role of phosphorus in Great Lakes eutrophication: Is there a controversy? J. Fish. Res. Board Can. 36: 286–288.

Phosphorus is undoubtedly the major plant nutrient controlling phytoplankton growth in the upper Great Lakes and the nutrient responsible for accelerated eutrophication in the lower Great Lakes. No studies published before 1970 provide conclusive evidence of the specific roles of phosphorus and other nutrients as growth limiting factors for phytoplankton. Improper citation of references can inadvertently cast doubt on the key role of phosphorus, or denigrate uncited work, depending on the reader's background.

Key words: phosphorus, nitrogen, eutrophication, phytoplankton, limiting nutrients, Lake Michigan, Lake Superior, Lake Huron

SCHELSKE, C. L. 1979. Role of phosphorus in Great Lakes eutrophication: Is there a controversy? J. Fish. Res. Board Can. 36: 286–288.

Le phosphore est sans doute le principal élément nutritif contrôlant la croissance du phytoplancton dans les Grands Lacs supérieurs et l'élément responsable de l'eutrophisation accélérée des Grands Lacs inférieurs. Aucune étude publiée avant 1970 ne présente de preuves concluantes des rôles spécifiques du phosphore et d'autres éléments nutritifs comme facteurs limitant la croissance du phytoplancton. Des références incorrectement citées peuvent, par inadvertance, faire douter du rôle-clé du phosphore ou peuvent dénigrer les travaux non cités, selon les antécédents des lecteurs.

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How "controversies" arise in science can be illustrated by the following: "Phosphorus has been found to be the nutrient most frequently limiting plant growth in the Great Lakes." (page 19, PLUARG July 1978 report to IJC) The statement without doubt is justified but could be questioned due to improper citation of references. In one reference (Beeton 1965) the word phosphorus could not be found because this paper considers nutrients indirectly. In the second reference (Dobson et al. 1974), the strongest supporting statement was ". . . this suggests that phosphate may well be a limiting factor for plankton growth in these two lakes," referring to Lakes Huron and Superior. Obviously a statement as conclusive as the one used in the PLUARG report is not justified based on inappropriate citation of references.

Two controversies can arise from these inaccuracies in literature citation. Persons not familiar with the literature, in examining the two "primary references," might quickly conclude that there is in fact no basis to state that phosphorus is the nutrient most frequently limiting plant growth. At the opposite extreme, persons familiar with the literature might conclude that other papers that state without reservation that phosphorus limits plant growth are not worthy of citation for some unknown reason. In either case a controversy can be created when undoubtedly one was not intended.

I was interested to see the statement that phosphorus limited plant growth knowing that less than 10 years ago there was in fact no supporting evidence in the literature and also knowing that this characteristic of the Great Lakes was questioned frequently before being accepted generally. Two references can be examined (Schindler 1971 and Likens 1972) for additional background on this point. Schindler's paper convincingly showed that there should not be a "carbon controversy" because phosphorus would be much more likely to be a limiting nutrient. Likewise several papers and the discussion by Vallentyne (p. 311) in Likens (1972) arrive at the same conclusion.

Direct experimental evidence that phosphorus limits plant growth in the Great Lakes did not appear in the literature until the 1970s. One paper was part of the symposium on the limiting nutrient controversy (Schelske and Stoermer 1972). Other early papers that showed that phosphorus is a limiting nutrient in Lake Michigan were those by Schelske and Stoermer (1971) and Thomas et al. (1975). Since then evidence that phosphorus limits phytoplankton growth has been obtained for Lake Superior (Schelske et al. 1972) and for

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Lake Huron (Lin and Schelske 1978 and Schelske et al. 1978). Direct experimental evidence that phosphorus is a growth limiting nutrient has been obtained at the species level (Stoermer et al. 1978). Some of these experiments have been designed so that the effects due to phosphorus could be tested statistically with probability levels of a phosphorus effect being >0.99 in many cases.

In addition to the effect of phosphorus additions alone on phytoplankton growth, interactions with chelating agents, trace metals, or both (Schelske et al. 1974; Lin and Schelske 1978; Schelske et al. 1978; Stoermer et al. 1978) increase the stimulatory effect of phosphorus on phytoplankton growth. These results suggest that the effect of phosphorus in the ecosystem may be greater due to synergistic interactions than might be predicted if only phosphorus were considered. An interaction of phosphorus and manganese on phytoplankton growth in Lake Superior has been reported (Shapiro and Glass 1975).

Nitrogen supplies do not limit phytoplankton growth in the upper lakes (Schelske et al. 1974; Lin and Schelske 1978; Stoermer et al. 1978; Schelske et al. 1978) and are only limiting in the lower lakes, Lake Erie and Lake Ontario, and other highly enriched areas where large supplies of phosphorus have promoted phytoplankton growth to the extent that a deficiency in nitrogen is created (Schelske and Roth 1973). In the Great Lakes, this condition is easily detected chemically from the presence of readily measured concentrations of soluble reactive phosphorus (Schelske et al. 1978) because supplies are greater than those that had been assimilated previously by phytoplankton.

Since 1970, adequate data have become available so the role of phosphorus in eutrophication of the Great Lakes can be inferred from environmental data. Before that Beeton (1969) stated with regard to Lake Michigan that "insufficient phosphorus data are available to show any change and the published data do not agree" and with respect to Lake Erie that "total phosphorus concentrations appear to have doubled between 1942 and 1958." After good data on phosphorus and standing crops of phytoplankton (primarily chlorophyll) became available it was possible to draw conclusions about the relationship between phosphorus and chlorophyll. It was stated "that particulate or total phosphorus are good measures of trophic state in the Great Lakes because phosphorus is the nutrient that limits phytoplankton growth and controls standing crops" (Schelske and Roth 1973, p. 68). These relationships are evident from unpublished manuscripts by H. Dobson and from published reports (Dobson et al. 1974; IJC report 1977, p. 553).

The scientific community still may not appreciate the extreme sensitivity of the Great Lakes, particularly the upper lakes, to phosphorus enrichment. Drastic biological and geochemical changes have been produced in Lake Michigan (Schelske and Stoermer 1971) as the result of increased phosphorus loadings. Increases in phytoplankton growth have resulted from single additions of 5 μg P/L, the smallest addition tested (Schelske et al. 1978; IJC 1977, p. 551). The minimum level for a response has not been tested for a spike treatment, although additions of 3 μg P/L have stimulated growth in treatments containing other nutrients (Lin and Schelske 1978). These experiments have been conducted by measuring growth responses of naturally occurring phytoplankton assemblages in lake water which is the most sensitive and reliable technique for assessing nutrient limitation in oligotrophic waters (Schelske et al. 1978).

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PERSPECTIVES

Freshwater Benthic Invertebrate Life Histories: Current Research and Future Needs

Proceedings of the Plenary Session of the 26th Annual Meeting of the North American Benthological Society, Winnipeg, Manitoba, May 10–12, 1978

EDITED BY DAVID M. ROSENBERG

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Introduction[1]

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THE North American Benthological Society, known as the Midwest Benthological Society until 1974, was formed in Havana, Illinois, in 1953. The purpose of the Society is to promote understanding of the benthic biological community and its role in aquatic ecosystems by providing media for exchange of information among its members. The annual meeting of the Society is one such medium. The papers that follow were presented at the Plenary Session of the 26th Annual Meeting of the Society held at the University of Manitoba, Winnipeg, from May 10 to 12, 1978.

The last few decades of ecological research have been marked by a shift in emphasis from natural history to numerical, quantitative approaches. These recent approaches often need detailed life history information but rarely have it. It is becoming more apparent that life history information will have to form a larger part of studies such as those seeking to explain community-level processes. Thus, choice of the Plenary Session theme was motivated by a desire to affirm the importance of life history studies to contemporary benthic science and to confirm that natural history approaches are alive and well despite the ascendancy of mathematical ecology.

The theme was developed by showing the relevance of life history information to major areas of benthic research today: taxonomy, sampling, production, feeding, bioassay, environmental disturbances, and management. The treatment is ended by a somewhat philosophical summary that identifies needs for future research.

Mr J. F. Flannagan, Dr O. A. Sæther, and I chose the Plenary Session theme. I thank the authors who participated and prepared papers for publication: Drs N. H. Anderson, E. F. Benfield, A. L. Buikema Jr., K. W. Cummins, D. M. Lehmkuhl, D. Malley, D. R. Oliver, J. B. Reynolds, V. H. Resh, T. F. Waters, and H. E. (Buster) Welch. Dr J. H. Mundie offered excellent advice on improving our treatment of the theme. Mss C. M. Anderson and A. J. Ratuski typed the many drafts. Ms J. Steeves and Mr A. P. Wiens helped with the proofreading.

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Sampling Variability and Life History Features: Basic Considerations in the Design of Aquatic Insect Studies[1]

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RESH, V. H. 1979. Sampling variability and life history features: basic considerations in the design of aquatic insect studies. J. Fish. Res. Board Can. 36: 290–311.

Sampling variability in benthic studies may result from sampling device operation, physical features of the environment, laboratory sorting procedures, and biological features of study populations. Selected factors and procedures that influence variability, samplers affected, and proposed remedies are presented. Consequences of not considering autecological components in sampling designs are illustrated by analysis of larval counts of *Cheumatopsyche pettiti* (Banks), a multiple cohort caddisfly with an aggregated population. The range of mean num-

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bers of *C. pettiti* was great with low sample numbers. Aggregation is more reliably measured at low sample numbers with the Index of Dispersion and the Mean Crowding Index than with the dispersion parameter k, the calculation of which from the maximum-likelihood equation, is integrally related to sample size. Nonrandom patterns of *C. pettiti* observed from samples collected in an Indiana, USA, stream riffle, may result from a failure to consider hyporheic distributions, spatial influences (*e.g.* sampling both favored and nonfavored microhabitats), instar-specific differences, and behavioral features. Variability in secondary production estimates of an aggregated population of *Ceraclea ancylus* (Vorhies) from a Kentucky, USA, stream indicated similar relationships to sample size.

The size of the mean, the degree of aggregation, and the desired precision of the mean estimate will influence the number of samples required to estimate densities of benthic populations. Sample size requirements calculated from data reported in previous studies were high to achieve accepted levels of precision. Habitat stratification may reduce the numbers of samples required. *Dicosmoecus gilvipes* (Hagen) exhibited nonaggregated patterns and required fewer samples to estimate density in uniform substrate areas of a California, USA, river pool than did aggregated populations in both mixed substrate areas and the entire pool. *Ceraclea ancylus* required fewer samples for density estimates in stratified (by habitat or substrate type) than unstratified habitats, the fewest samples being necessary when the individual stone was the sampling unit. Judicious choice of study populations may permit larger numbers of samples to be collected and processed with reduced cost, as an alternative to stratification. Larvae of *C. ancylus* and *D. gilvipes* could be separated in the field; density underestimation due to a hyporheic population component was eliminated because of surface dwelling behavior or by choice of study sites; and compounded spatial distributions due to co-occurring instar-specific patterns were absent because the populations have a single cohort.

Larger numbers of samples may be necessary than are generally taken in benthic studies. Further research is needed to assess variability in secondary production estimates and community diversity analyses. Improved methods for substrate surface area estimation and increased use of experimental approaches and sequential sampling techniques should be considered in future benthic sampling designs.

Key words: sampling, benthos, aquatic, macroinvertebrate, Trichoptera, insect, experimental design, autecology, life history, variability

RESH, V. H. 1979. Sampling variability and life history features: basic considerations in the design of aquatic insect studies. J. Fish. Res. Board Can. 36: 290–311.

La variabilité de l'échantillonnage dans les études sur la faune benthique peut être due au fonctionnement de l'échantillonneur, aux caractéristiques physiques de l'environnement, aux méthodes de tri au laboratoire et aux caractères biologiques des populations étudiées. L'auteur décrit certains facteurs et méthodes agissant sur la variabilité, les échantillonneurs affectés et les remèdes proposés. A l'aide d'une analyse des comptages de larves de *Cheumatopsyche pettiti* (Banks), une phrygane à cohortes multiples constituant une population agrégée, il illustre ce qui peut arriver quand on ne tient pas compte des éléments autécologiques dans la conception de l'échantillonnage. Les nombres moyens de *C. pettiti* sont répartis sur une gamme étendue quand les échantillons sont de petite taille. Dans ces cas, l'agrégation est mesurée avec plus de fiabilité à l'aide de l'indice de dispersion et de l'indice de tassement moyen qu'à l'aide du paramètre de dispersion k, dont le calcul dérivé de l'équation de probabilité maximale est intégralement lié à la taille de l'échantillon. Les modalités non aléatoires de répartition de *C. pettiti* observées dans des échantillons prélevés dans un radier d'un cours d'eau de l'Indiana, E.-U., peuvent résulter d'un manque à tenir compte des distributions hyporhéiques, des influences spatiales (e.g. échantillonnage des micro-habitats favorisés aussi bien que non favorisés), des différences particulières aux instars et des caractéristiques de comportement. La variabilité observée dans les estimations de production secondaire d'une population agrégée de *Ceraclea ancylus* (Vorhies) d'un cours d'eau du Kentucky, E.-U., montre des relations semblables avec la taille de l échantillon.

La grandeur de la moyenne, le degré d'agrégation et la précision désirée dans l'estimation de la moyenne influeront sur le nombre d'échantillons requis pour estimer la densité des populations benthiques. Les exigences quant à la taille des échantillons calculées à partir de données publiées sont grandes si l'on veut atteindre des niveaux acceptables de précision. La stratification des habitats peut réduire le nombre d'échantillons requis. *Discomoecus gilvipes* (Hagen) ne forme pas de populations agrégées et nécessite moins d'échantillons, lorsqu'il s'agit d'estimer la densité dans des régions de substrat uniforme d'une fosse, dans une rivière de la Californie, E.-U., comparativement à des populations agrégées tant dans les régions de substrats mixtes que dans la fosse entière. *Ceraclea ancylus* nécessite un nombre moindre d'échantillons pour l'estimation de la densité dans des habitats stratifiés (par habitat ou par type de substrat) que dans des habitats non stratifiés, le minimum d'échantillons étant nécessaire quand l'unité d'échantillonnage est une pierre individuelle. Grâce à un choix judicieux des populations à

étudier, on pourra recueillir et traiter un plus grande nombre d'échantillons à moindre coût, comme solution de remplacement de la stratification. Les larves de *C. ancylus* et *D. gilvipes* ont pu être séparées sur le terrain; la sous-estimation de la densité causée par l'élément hyporhéique de la population a été éliminée par suite d'un mode de vie en surface ou par le choix des sites d'études; enfin, les distributions spatiales cumulatives résultant d'une co-habitation particulière aux instars étaient absentes car les populations ne comprenaient qu'une cohorte.

Il est donc possible qu'on ait besoin d'un plus grand nombre d'échantillons que ceux généralement prélevés lors d'études benthiques. Il faudra des recherches plus poussées dans le but d'évaluer la variabilité des estimations de la production secondaire et des analyses de diversité des communautés. Dans la conception future de l'échantillonnage benthique, il faudra envisager des méthodes améliorées d'estimation de la superficie du substrat et utiliser davantage des approches expérimentales et des techniques d'échantillonnage continu.

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For many naturalists and ecologists involved in research 20–30 yr ago, the study of life histories was considered an appropriate research endeavor in itself, with the autecological information obtained not necessarily intended for immediate systematic or ecological application. The importance of this type of research to ecologists of that era is evidenced by the Ecological Society of America's formation of "The Committee on Ecological Life Histories," whose sole purpose was to stimulate further interest in life history studies by publishing selective bibliographies and outlines for studies of *typical ecological life forms* (Ecol. Soc. Amer. 1948–57, e.g. Linsley et al. 1952).

In recent years, however, there has been a change in the emphasis of ecological research, namely a shift from descriptive autecology to quantitative methods including systems analysis and mathematical modeling (Gilbert et al. 1976; Pielou 1977). Ecological studies of aquatic insects have also been influenced along quantitative lines, for example, by the application of macrobenthic community analysis to the evaluation of environmental quality.

Based on current literature and papers presented at society meetings, it is apparent that descriptive life history studies of aquatic insects have declined in both research priority and popularity. This does not mean life history studies are no longer being done, but rather, they are more often based on results obtained from a sampling design developed for an alternative purpose. For example, as part of a study evaluating the effects of oil spills on benthic communities (Rosenberg and Wiens 1976), the life history patterns of two chironomid species were elucidated (Rosenberg et al. 1977a). The results of these and other studies (Rosenberg et al. 1977b; Welch 1976) suggest that if the converse situation was generally applied to benthic studies (i.e. if life history information was used in developing sampling designs), research objectives might be more easily, or even better, fulfilled.

The purpose of this paper is threefold: (1) to review some sources of error in benthic sampling; (2) to give examples of how these factors can affect sampling reliability; and (3) to examine the role that life history information can play in developing appropriate sampling designs for benthic research.

The approach used in this analysis has been (a) to conduct field studies that examine and illustrate basic problems in designing sampling regimes for aquatic insect research and the implications of sampling variability on data interpretation in these studies; and (b) to reevaluate the results of previously published quantitative studies with the above purpose in mind. In some cases, hypothetically derived data may have better fulfilled certain statistical assumptions than field-collected data and allowed a more sophisticated level of analysis. However, discussions of sampling variability designed along theoretical lines often seem to lack relevance to field biologists. In addition, they often include detailed statistical treatments that may not be clearly understood by many of the researchers who are directly involved in the design and implementation of aquatic sampling programs. While this presentation is not totally free of mathematical jargon, it attempts to graphically and simply illustrate the sampling problems of aquatic biologists along with the important interaction between sampling variability and life history considerations.

Benthic Sampling Problems: A Review of Some Sources of Error

Sampling variability can result from the choice and operation of sampling devices, physical features of the environment (Table 1), field and laboratory sorting procedures (Table 2), and biological features of the study organisms themselves (Table 3). The choice of an appropriate sampling device from the literaliy hundreds of types and modifications available (Elliott and Tullett 1978) should be a function of the physical characteristics of the habitat, the types of organisms under examination, and the objectives of the experimental design (e.g. see Merritt et al. 1978, table 3A). While there is continued need for improvement in the design of sampling devices and the development of corrective measures for various mechanical problems (Table 1A), the most severe limitation in current benthic studies is the inability to consistently take samples of known unit, especially with regard to the surface area of contained substrate particles. The quantification of surface area in ecological studies may be as critical a parameter as the treatment of volume or

TABLE 1. Selected examples of factors that affect benthic sampling devices and may result in sampling bias.

Factor	Samplers affected	Problems created	Remedy
		A. Factors related to characteristics of the samplers	
Backwash created in sampler by water not being able to pass through net	Netted and kick samplers	4–30% loss of benthos around sides of sampler (Badcock 1949; Macan 1958; Mundie 1971; Frost et al. 1971)	Increase the net's surface area and/or decrease size of net opening (Macan 1958); use enclosed double netted sampler (Mundie 1971); alternatively use a hand-operated Ekman grab or cylinder box sampler (Hynes 1971)
Washout of surface organisms upon placement of sampler	Hess sampler	Turbulence scours substrate surface (Macan 1958)	Use permeable sides (Waters and Knapp 1961)
Disruption of substrate surface by shockwave when sampler strikes bottom	Corer and Grab samplers	Loss of small organisms and surface dwellers (Flannagan 1970; Howmiller 1971; Milbrink and Wiederholm 1973)	Modify Ekman grab by removing screens and incorporating heavier materials in design (Burton and Flannagan 1973); alternatively use a pneumatic grab (Murray and Charles 1975), a box sampler (Jonasson and Olausson 1966; Farris and Crezee 1976), or a modified corer (Brinkhurst et al. 1969; Kajak 1963, 1971)
Disturbance of biota	Surber sampler and Allan grab	Underestimation of biota due to disruption when sampler is set in place (Surber: Kroger 1972; Allan grab: Kajak 1971)	Modify Allan grab by adding screened openings on top
	Shovel sampler	Loss of motile organisms (Macan 1958; Hynes 1970)	
Variable depth of penetration into substrate by sampler	Grabs	Inconsistent volume of sediment sampled; loss due to overfilling (Flannagan 1970) or incomplete closure (Kajak 1963; Gale 1971)	Leave 5-cm space above substrate (Flannagan 1970); alternatively use a corer whenever possible (Kajak 1963; Gale 1971)
	Surber	Failure to consider stream hyporheic zone	Two stage sampling, surface and hyporheic
Variable area sampled	Shovel sampler	Area sampled laterally is variable (Macan 1958)	
Sampler mesh size too coarse	Netted samplers	Early instars, small and slender organisms missed (Zelt and Clifford 1972; Frost et al. 1971; Mundie 1971; DeBovee et al. 1974)	Finer mesh, or preferably a double bag sampler (Macan 1958; Frost et al. 1971; Mundie 1971; Zelt and Clifford 1972; Barber and Kevern 1974)
Sampler mesh too fine	Netted samplers	May cause backwash (see above)	Coarser mesh as in double bag samplers
Sampler dimension too large	All samplers	Increases sorting time; may not detect population aggregations (Elliott 1977)	Smaller samples (Elliott 1977; Voshell and Simmons 1977)
	Grab samplers and corers	Inefficient cost/sample ratio (Karlsson et al. 1976)	When density > several hundred/m^2 use corer, when < use Ekman grab (Kajak 1963); alternatively use multiple corer (Brinkhurst et al. 1969; Flannagan 1970; Hakala 1971)
Sampler dimension too small	All samplers	May not detect aggregations; variability increased due to edge effect (Elliott 1977)	Use nested sampler to determine optimal sampler dimension
Operator inconsistency	All samplers	Systematic error in population estimates (Needham and Usinger 1956)	Single operator; or correction factor for each operator (Chutter 1972)

TABLE 1 (*Concluded*)

Factor	Samplers affected	Problems created	Remedy
		B. Factors related to characteristics of the environment	
Water depth limitations in lotic environments	Surber and Hess samplers	Surber sampler limited to <30 cm depth (Macan 1958; Albrecht 1959; Chutter 1972)	From 0.5 to 4 m use an airlift sampler (Mackey 1972; Pearson et al. 1973); 0.4 to 10 m deep, SCUBA and dome suction sampler (Gale and Thompson 1975) or modified Hess sampler (Rabeni and Gibbs 1978); or use a modified Allan hand operated grab (Allan 1952; Kajak 1971) or bottombasket samplers (e.g. Crossman and Cairns 1974; Rabeni and Gibbs 1978)
Substrate — stony	Grab samplers, corers	Grabs may not close (Kajak 1971); cylinder sampler cannot penetrate (Ulfstrand 1968b)	Substitute airlift or dome suction sampler and artificial substrate as above
Substrate — mixed	Grab samplers, corers	Differential penetration	Flannagan (1970) recommends specific samplers for different substrate types; stratified sampling (Scherba and Gallucci 1976)
Current too slow	Surber and kick samplers	Organisms do not drift into net	Enclosed sampler such as modified Surber or Hess sampler (Leonard 1939; Waters and Knapp 1961)
Current too fast	Netted samplers	Backwash, resulting in a loss of organisms	Substitute a modified sampler with controlled flow (Mundie 1971)
Current fluctuations	All samplers	Rapid change in flow may scour study area	
Low air temperatures	Netted samplers	Samples freeze in net before organisms are removed	Catch bottle or a zippered net (Waters and Knapp 1961; Lane 1974)
Sampling in vegetation	All samplers	Loss of organisms during removal; inability to close sampler	Use samplers described by Welch (1948), Macan (1949), Gerking (1957), Gillespie and Brown (1966), Mackie and Qadri (1971), Minto (1977), or artificial vegetation (Glime and Clemons 1972; Higler 1977; Macan 1977a)
Sampling in open water	Lotic: drift samplers; lentic: all samplers	Lotic: net clogging and changes in current and flow pattern affect estimation of water volume sampled (Pearson and Kramer 1969); lentic: sampling a consistent volume of water; scattering of organisms (Legner et al. 1975)	Lotic: use Parshall flume drift net (Hales and Gaufin 1969) or waterwheel drift sampler (Pearson and Kramer 1969); lentic: use column samplers (e.g. Legner et al. 1975; Enfield and Pritchard 1977; Henrickson and Oscarson 1978) or pull-up trap (Higer and Kolipinski 1967)
Habitat small	All samplers	Sampling destroys habitat (Chutter 1972; Mason 1976)	Smaller sampler dimension; artificial substrates (Glime and Clemons 1972; Macan 1976, 1977a,b)
Water chemistry	All samplers	Presence of springs, man-made outfalls, and other conditions may influence microhabitat distribution of biota	Reconnaissance

mass (Dahl 1973) and has been suggested as a necessary consideration in benthic studies of both marine (Dahl 1973; Fricke and Thum 1976; Stearn et al. 1977) and freshwater (Calow 1972) environments. When the density of organisms is examined with reference to the area or volume of the substrate rather than the area actually available in terms of stone surface, mean density estimates will have a variance with two components: that due to the degree of population aggregation and that due to the fact that each sample may contain different amounts of stone surface; only that component due to aggregation is usually of interest in ecological

TABLE 2. Selected examples of factors related to benthic sorting procedures that may result in sampling bias.

Procedure	Potential problems	Remedy or comment
Preservation	Alcohol preservative may cause a weight loss (Leonard 1939; Howmiller 1972; Stanford 1973; Donald and Paterson 1977; Wiederholm and Eriksson 1977)	Weight loss stabilizes over time (Howmiller 1972) so correction factors may be used (Leonard 1939; Stanford 1973); alternatively use other preservatives (Donald and Paterson 1977) or other weighing methods (Wiederholm and Eriksson 1977)
Live sorting by electroshocking	Selective for large organisms (Bayless 1961)	Useful technique when large amounts of organic matter present
Sieves too coarse	Underestimation of numbers; misinterpretation of life histories (Jonasson 1955)	Use finer mesh (Jonasson 1955; Frost et al. 1971; DeBovee et al. 1974; Shiozawa and Barnes 1977)
Sieving	Physical damage to specimens (Hynes 1971)	Sieve under water, without spraying directly on top (Hynes 1971); elutriation may be preferable (Stewart 1975)
Flotation	Flotation time varies with preservative used, taxa present, and instar within same taxa (Flannagan 1973)	Live flotation or formalin and sugar solution maximize flotation time (Anderson 1959; Flannagan 1973)
	Selective against case bearing caddisflies and mollusks (Flannagan 1973; Hynes 1971) and microbenthos (Stanczykowska 1966)	Repeated flotation with freshwater washes (Anderson 1959) and examination of remaining material may be necessary
Subsampling	Rare organisms or life history stages may be missed	Subsample size should be adjusted so that smallest taxon counted > 100, Lund et al. 1958)
Counting	Smaller specimens may be missed	Maximum counting efficiency 25× magnification with transmitted light (Frost 1971)

analyses (Calow 1972). Some efforts have been made to analyze surface substrate heterogeneity (Cummins 1962; Fricke and Thum 1976; Stearn et al. 1977; Gore 1978), an indirect approach to solving this problem. However, these techniques must be expanded and other approaches (e.g. substrate implants with natural habitat [e.g. Minshall and Minshall 1977] or individual stone sampling, using appropriate surface area methods [e.g. Calow 1972]) must be considered if this problem is to be resolved.

In addition, two other areas require much greater attention in benthic studies. First, more emphasis must be placed on evaluating the efficiency of field and laboratory procedures for sorting organisms from the substrate. For example, unless samples are meticulously hand-picked, some underestimation of total numbers will invariably result. It is important that the extraction procedures keep such losses to a minimum so that density estimates are not significantly altered or that certain size-classes are not selectively sorted and thus influence life cycle interpretation.

If bias due to sampling and sorting procedures were accounted for, how much of the total sampling variability would be explained? Many past studies of sampling variability imply that mechanical factors are mainly responsible for variability (e.g. Needham and Usinger 1956), while neglecting biological components that may also be involved. This, the second area requiring increased attention, involves consideration of whether the population universe as designated by the sampling design is the same or different than the true population universe as determined by biological features of the species under study. In the remainder of this paper, the influence of these biological features on sampling variability (Table 3) and methods for reducing or at least accounting for sample bias due to these factors will be examined by field studies and data analysis techniques.

Spatial Heterogeneity and Sampling Variability

The following study was designed to examine how sampling variability may be influenced by a failure to consider biological features of the study population and how this variability may influence the estimation of population parameters.

A riffle of near uniform depth (10–12 cm) and substrate particle size (majority of substrate particles 4–12 cm diam [ϕ,-5; ϕ,-6], see Hynes 1970, table I, 4) located in Rock Creek, Carroll Co., Ind., was divided into a series of 30.5 × 61.0 cm (1 × 2 ft) rectangular quadrats. Locations within this grid were chosen at random and two Surber samplers were placed side by side with both samples (A and B) collected at the same time. The substrate was removed to a depth of 10 cm. These paired samples were taken at 26 randomly selected locations throughout the riffle between June 5 and 6, 1975. The number of larvae of the multiple cohort hydropsychid caddisfly, *Cheumatopsyche pettiti* (Banks), a species widely distributed throughout eastern North America and commonly encountered in benthic collections, was counted for each sample.

TABLE 3. Factors related to biological characteristics of the organisms under study that may result in sampling bias.

Factor	Samplers affected	Problems created	Remedy
Lithophilic behavior	All samplers	Loss of organisms due to concealment or attachment (Macan 1958; Hynes 1970; Frost et al. 1971; Lavery and Costa 1972; Pearson et al. 1973)	Dip rocks in dilute HCl/alcohol (Britt 1955); direct examination of substrate (Lavery and Costa 1972)
Hyporheic distribution	Surber, Hess samplers	Inconsistent underestimations of population density (Radford and Hartland-Rowe 1971; Hynes et al. 1976); failure to find species that are primarily hyporheically distributed (Hynes 1970)	Determine presence of hyporheic fauna using samplers described by Williams and Hynes (1974) and Hynes (1974)
Motility of organisms	All samplers	Organisms flee when disturbed	
	Artificial substrates	Organisms flee from sampler when artificial substrate is removed (Hilsenhoff 1969; Mason et al. 1973)	Use a net to retain organisms in artificial substrates (Hilsenhoff 1969)
	Frozen core samplers	Organisms flee cold, escaping capture (Stocker and Williams 1972; Walkotten 1976)	
Population movements	All samplers	Sampling regimes and techniques not applicable through life cycle stage (e.g. planktonic first instar larvae of chironomids) (Davies 1976)	Use activity trap (Davies 1976)
		Prepupation movements of caddisfly larvae (Cummins 1964; Anderson 1967; Otto and Svensson 1976; Wiggins 1977) and pre-emergence movements of mayfly nymphs (Harker 1953)	Two-stage sampling
Attractability (or catchability) of certain species	All samplers	Less motile species may appear more abundant than they really are in relation to more motile species	
	Artificial substrates	Numbers and kinds of organisms in artificial substrates differ from that found in benthos (McDaniel 1974; Minshall and Minshall 1977)	Use substrate matching that found in stream bed (Glime and Clemons 1972; Minshall and Minshall 1977) or a type generally attractive to stream organisms (Macan and Kitching 1976; Macan 1977a); bottom basket samplers may be more reliable than floating samplers (Crossman and Cairns 1974); exposure time for colonization before removal is critical (Mason et al. 1973)
Spatial distribution patterns	All samplers	Nonrandom patterns require greater numbers of samples to estimate density with the same precision as for random distributed populations. Aggregations may result from microhabitat preferences of substrate, current, food source, etc. or behavioral interactions. Benthic populations generally exhibit aggregated spatial distribution patterns	See text

One might expect that the number of larvae in each of these paired samples would be the same or very similar. However, equal numbers of individuals were rarely found in adjacent samples (Fig. 1; those samples with identical larval counts would lie directly on the dotted line). In fact, while some pairs have similar numbers of larvae in each sample, others vary greatly. The frequency distribution of the larval counts in each sample indicates a nonrandom pattern (Fig. 2) that best agrees with that predicted for a negative binominal distribution ($T = 86.75$, standard error of $T \approx 222.7$, $P > 0.95$).

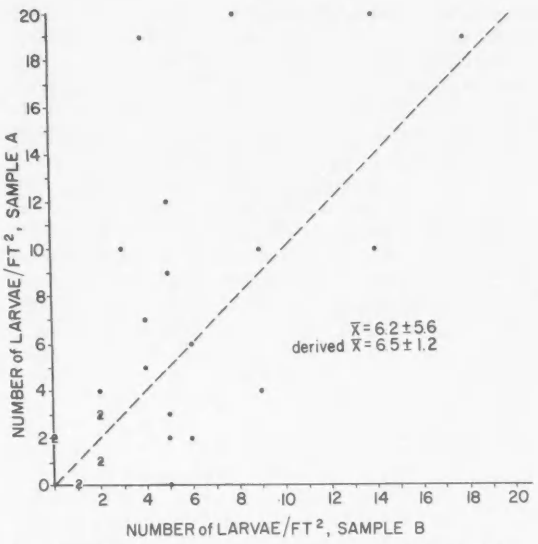

FIG. 1. Number of *Cheumatopsyche pettiti* (Banks) larvae per square foot (1 ft² = 0.09 m²) in Rock Creek, Carroll Co., Ind. Coordinate points represent replicate samples. Dotted numbers refer to multiple points with the same coordinate. Derived mean calculated using a logarithmic transformation.

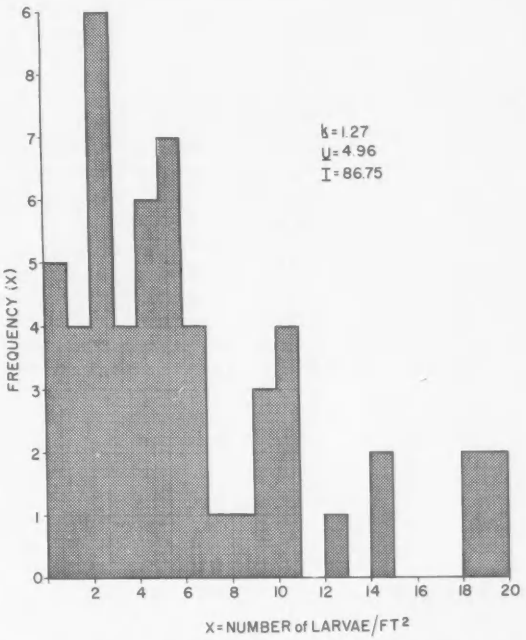

FIG. 2. Frequency distribution of *C. pettiti* larvae per square foot sample in Rock Creek. Statistics *k*, *U*, and *T* were used to test conformance to a negative binomial distribution pattern.

SAMPLING VARIABILITY AND THE INTERPRETATION OF POPULATION DENSITY

To illustrate the relationship between mean density and the number of samples collected (or sample size), a data matrix was constructed using the number of *C. pettiti* in each of the 52 quantitative samples. A hypothetical sampling regime was developed in which means and variances were calculated for sample sizes ranging from 2 to 52 and arranged in increments of 2. That is, in the first analysis two samples were drawn at random and the mean and variance calculated. In the second analysis, four samples were drawn. This sequence was continued for sample sizes of 6, 8, 10 (etc.) until 52 samples were included. Numbers were replaced in the matrix and could be drawn and included in the calculations for a given value of n more than once. The procedure was repeated 30 times for each sample size to determine variation in the calculation of density. This treatment resulted in estimates of mean and variance (and spatial distribution statistics discussed below) for 780 individual data sets (26 sample size categories, 30 replicates).

At small sample sizes the range of possible sample means (Fig. 3) and variance estimates is great. For example, with a sample size of 2, calculated means range from 1.5 to 14.5 larvae/ft² (1 ft² = 0.09 m²), compared with the sample mean of 6.2. Likewise, variances with a sample size of 2 range from 0 to 162. Decreases in the range of sample means are evident with increased sample size (Fig. 3). This relationship can also be shown by calculations of sample size statistics. Requisite numbers of samples based on a population mean of 6.2 (Fig. 1) and a negative binomial distribution (Fig. 2) are presented in Table 4. With a sample size of 24 (95% confidence limits ± 40% of the mean) the calculated means for the 30 replicates (Fig. 3) range between 4.5 and 9.0 larvae/sample (≈95% of the 30 replicates range from 5.0 to 8.7), estimates far less variable than those observed for lower sample sizes.

Nonrandom distribution patterns of benthic macroinvertebrates, as exhibited by *C. pettiti* (Fig. 2), usually cause greater variability in sample counts than randomly distributed populations (Watanabe and Harada 1976; Mason 1976). In fact, an aggregated distribution is probably the most common pattern exhibited by aquatic insect populations (Mottley et al. 1938; Needham and Usinger 1956; Allen 1959; Chutter and Noble 1966; Egglishaw 1969; Sugimoto 1969; Elliott 1977; Minshall and Minshall 1977). These spatial patterns may result from either microenvironmental variation in which one habitat (or microhabitat) is favored over another or from behavioral interactions that may cause individuals to aggregate independently of environ-

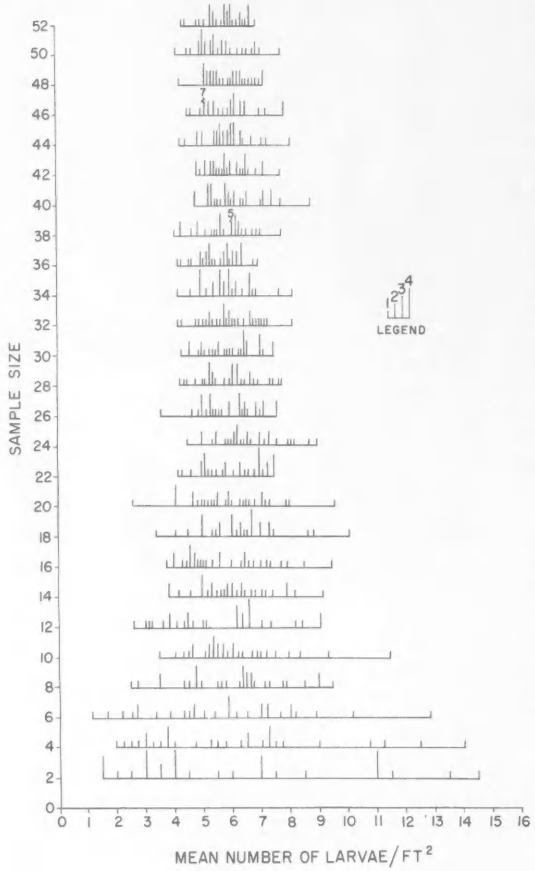

FIG. 3. Sample size influence on mean number of *C. pettiti* larvae per square foot sample in Rock Creek. For each sample size the horizontal line refers to the range of means calculated, with the vertical lines referring to the number of times an individual mean (to the nearest tenth) was calculated.

mental factors. For instance, Alley and Anderson (1968) reported that negative binomial distribution patterns (e.g. Fig. 2) are typical of populations in which one or a few environmental factors disproportionately influence spatial distribution.

Several biological features could account for the nonrandom spatial distribution patterns and sampling variability observed in the *C. pettiti* populations including the following. (1) *Hyporheic component* — Sampling was confined to the upper 10 cm of substrate, although *Cheumatopsyche* (Williams and Hynes 1974) and other benthic species often occur deep within the hyporheic (Coleman and Hynes 1970; Hynes 1970; Hynes et al. 1976). Failure to consider the three dimensional aspect of spatial distribution in the *C. pettiti* population could have caused inconsistent underestimations of population density, resulting in a nonrandom distribution pattern. (2) *Spatial influences* — Net-spinning caddisfly larvae such as *C. pettiti* orient themselves to optimal current and feeding conditions (Williams and Hynes 1973; Wallace 1975); therefore, sampling both favored and nonfavored microhabitats may result in apparent patchiness. In addition, there may be longitudinal differences in spatial distributions, even within a uniform riffle (Mason 1976). (3) *Instar differences* — A failure to differentiate between instar-specific patterns in a multicohort population may result in a misinterpretation of spatial distribution patterns. All five larval instars of *C. pettiti* coexist in the Rock Creek riffle; each instar has a different filter mesh size and possibly a different spatial distribution pattern. In addition, early instar larvae may be clumped because individuals are dispersing from an egg mass. Changes in spatial distribution patterns over the life cycle are known for other caddisflies (Resh 1977), mayflies (Elliott 1977), and chironomids (Thut 1969; Shiozawa and Barnes 1977; McLaughlan 1977). In addition, there may be lateral movements and relocation of final instar *Cheumatopsyche* larvae as reported for other species of lotic caddisflies (Anderson 1967; Hultin *et al.* 1969; Otto 1971; Otto and Svensson 1976; Iverson 1976; Wiggins 1977) and other aquatic insects (Harker 1953; Ulfstrand 1968a; Hayden and Clifford 1974). (4) *Behavioral factors* — Aggression by *Cheumatopsyche* larvae (Glass and Bovbjerg 1969) may produce uniform distributions within a larval group, but if larvae are randomly distributed by groups, clumped patterns may appear to be present.

Past studies have examined sampling variability in both populations (Allen 1959; Mason 1976; Watanabe and Harada 1976) and communities (Needham and Usinger 1956; Chutter and Noble 1966; Chutter 1972; Mason 1976; Watanabe and Harada 1976) of aquatic macroinvertebrates. In each case the total number of individuals collected varied greatly from sample to sample. These studies should have had a profound effect on the sampling design of benthic studies. However, this has not happened. From studies published in refereed journals to mimeographed reports of environmental impact statements, the same trend is apparent: quantitative studies are often based on very few benthic samples. Small numbers of samples may be sufficient to provide a preliminary listing of species present (Needham and Usinger 1956), although problems in aquatic insect identification may limit the usefulness of such a list (Resh and Unzicker 1975). However, these few samples will almost certainly be insufficient for statistical analysis and accurate data interpretation.

SAMPLING VARIABILITY AND INDICES OF DISPERSION

The spatial arrangement of individuals may be of prime importance in understanding the ecology of a

TABLE 4. Number of samples (n) necessary to obtain an estimate of the population mean of *Cheumatopsyche pettiti* in Rock Creek. Sample size was calculated using the general formula and the formula applicable when a negative binomial distribution was a suitable model for the series (Elliott 1977).

Desired precision	n calculated by general formula	n calculated for negative binomial formula
95% confidence limits ±10%	327	379
" " " ±20%	82	95
" " " ±30%	37	43
" " " ±40%	21	24

population because this pattern may reflect factors that influence the population's existence in nature (Patil and Stiteler 1974). Spatial distribution patterns in almost all previous aquatic insect studies have been described simply as random or nonrandom and neither the degree of dispersion nor conformance to specific distribution models has been generally tested.

Values for many of the indices of spatial dispersion that are appropriate for benthic studies (e.g. Elliott 1977, tables 11, 12) unfortunately depend on the number of sampling units (Green 1966; Elliott 1977). This dependence can be illustrated by calculating the commonly used dispersion parameter, k, for each of the 30 replicates of the *C. pettiti* data (Fig. 2), (sample sizes $n = 2$ to $n = 52$). k can be calculated using the maximum-likelihood equation (from Southwood 1966; Elliott 1977):

$$n \log_e\left(1 + \frac{\bar{x}}{k}\right) = \Sigma\left(\frac{A(x)}{k + x}\right)$$

where n = the total number of sampling units, $\log_e$ = the natural (Napierian) logarithm, $A(x)$ = the total number of counts exceeding (x), and $\bar{x}$ = the mean. This equation is solved by iteration (i.e. different values of k are tried until the equation is balanced). Non-aggregated distributions are assumed when $k > 8$ and approaches ∞ (Southwood 1966). With fewer numbers of samples (Fig. 4), k approaches 0 indicating possible conformance of the data to a logarithmic distribution. As sample number increases (Fig. 4), more k estimates approach 2 indicating conformance to a negative binomial distribution (Southwood 1966). The few counts of k presented for the smaller sample sizes (e.g. 3 at a sample size of 2, 4 at a sample size of 4) represent the number of the 30 replicates for each sample size that indicated nonrandom distributions ($k < 8$; Fig. 4).

Two additional indices were calculated with the same data for comparison with k. The Index of Dispersion (I) was calculated as

$$I = \frac{s^2}{\bar{x}}$$

where s^2 = the variance; nonrandom distributions are indicated by $I > 1$ through $I = \Sigma x$ (Elliott 1977). The ratio of mean crowding to mean density or "patchiness," an index first proposed by Lloyd (1967), was also calculated. Mean crowding (x^*) is estimated as

$$x^* = \bar{x} + \left(\frac{s^2}{\bar{x}} - 1\right)$$

where $x^*/\bar{x}$ is a measure of patchiness with $x^*/\bar{x} > 1$ indicating a nonrandom distribution pattern (Lloyd 1967; Iwao 1968).

If the percentage of samples indicating a nonrandom distribution is determined using I, $x^*/\bar{x}$, and k, and compared for each of the 30 replicates over a range of sample sizes ($n = 2$ to $n = 52$), consistent indications of nonrandomness appear at a lower sample size for I and $x^*/\bar{x}$ than they do for k (Fig. 5). Note that 42 samples were required before equivalent results were obtained for all three measurements of clumping (Fig. 5). The results of this study reaffirm that k is as integrally related to sample size as are the mean estimates illustrated in Fig. 3. The calculation of I and $x^*/\bar{x}$ is simpler than the calculation of k. However, neither is as useful as k in measuring the degree of clumping or in determining conformance to a specific distribution model (Elliott 1977).

Sampling Variability and Secondary Production Estimates

The variability in estimating population density of *C. pettiti* as a function of sample size (Fig. 3) illustrates a sampling problem that is confined to a single time period. However, many ecological studies of aquatic insects, such as the estimation of secondary production have objectives that require repeated sampling of a population. How are production studies affected by populations with nonrandom distribution patterns and the number of samples collected? To examine this interaction, Resh and Newhouse (unpublished data) analyzed the results obtained in a secondary production study of *Ceraclea ancylus* (Vorhies), a leptocerid caddisfly.

In the original *C. ancylus* study (Resh 1977), quadrat samples were collected along stream transects at periodic intervals over an annual cycle. For the present analysis, all transect samples were arranged in a single

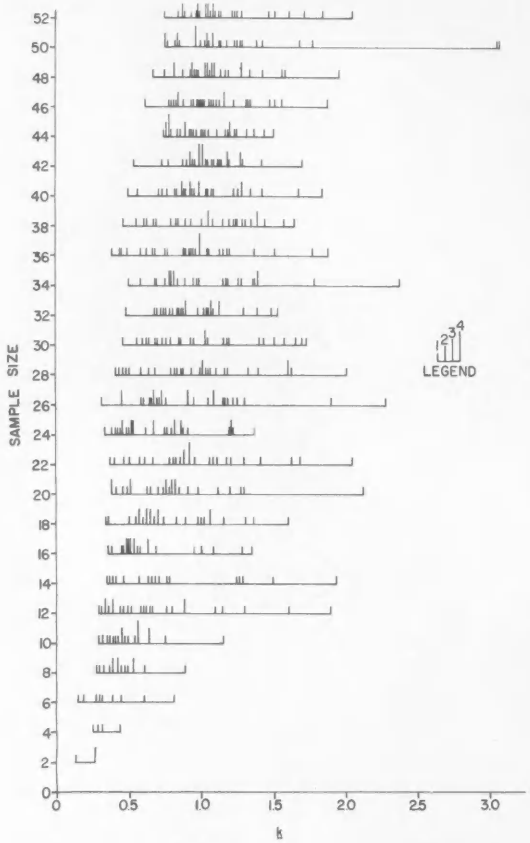

FIG. 4. Number of samples with nonrandom distributions and sample size influence on the value of k for the *C. pettiti* population in Rock Creek. For each sample size the horizontal line refers to the range of k values calculated, with the vertical line referring to the number of times an individual value of k (to the nearest tenth) was calculated. $k > 8 \rightarrow \infty$ were considered as random distributions (Southwood 1966) and were not plotted.

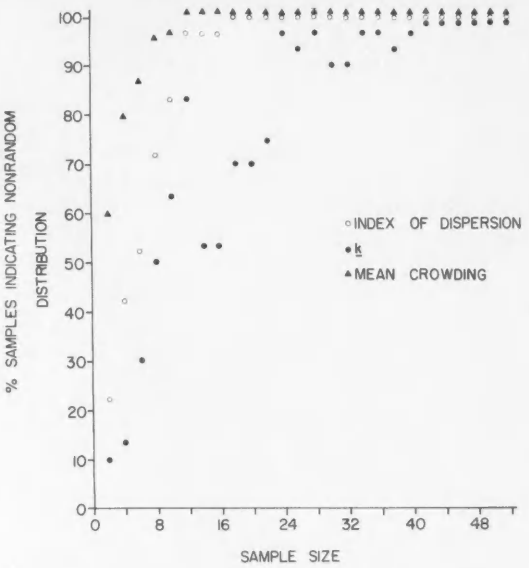

FIG. 5. Comparison of k, mean crowding ($x^*/\bar{x}$), and the Index of Dispersion (I) in terms of percentage of samples indicating nonrandom distributions [χ^2 test for I, $P > 0.05$ (Elliott 1977), $x^*/\bar{x} > 1$ (Lloyd 1967), and $k < 8$ (Southwood 1966)].

matrix by sampling date. Mean individual weights (MIW) and mean standing stock estimates were then calculated by drawing samples at random for each successive date. Sample sizes for these estimates ranged from $n = 1$ to $n = 69$. Secondary production was then calculated by the instantaneous growth method (Ricker 1968; Resh 1977, table 3). For example, at $n = 1$, a single sample was drawn at random for each sampling date and secondary production was calculated over the annual cycle. This was then repeated for $n = 2$ (two samples were drawn at random for each sampling date, a mean estimated, and production calculated). At $n = 69$ all transect collected samples were included in the calculation of the production estimates. Samples were not replaced in the matrix. For each value of n, randomized secondary production calculations were repeated 30 times, resulting in 2070 individual estimates. A coefficient of variation was then calculated for the 30 secondary production estimates for each sample size, from $n = 1$ to $n = 69$ (Fig. 6). At low sample sizes, there is a great deal of variability in each of the groups of 30 secondary production estimates (Fig. 6). This entire analysis was then repeated a second time with the same results. Like *Cheumatopsyche pettiti*, the *Ceraclea ancylus* population has an aggregated distribution pattern (Resh 1977) and requires larger numbers of samples to obtain acceptable minimum confidence limits for mean counts than would be necessary for a nonaggregated population. Production studies on denser, less aggregated populations, however, would tend to exhibit lower variability.

Effects of spatial variability on estimates of secondary production have not previously been considered in detail. However, it is obvious from the above examples that when these estimates are based on a small number of samples per sampling interval, a common practice in benthic studies, gross errors in interpreting the energetics of benthic populations may result.

Requisite Number of Samples in Benthic Studies

In both the *Cheumatopsyche pettiti* and *Ceraclea ancylus* variability examples presented above, I have

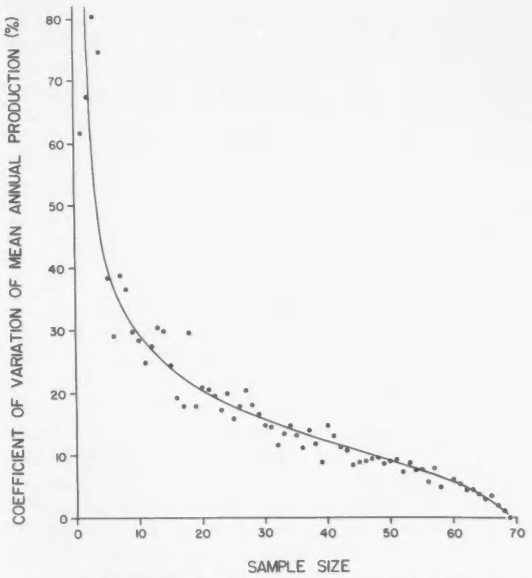

FIG. 6. Coefficient of variation (C.V. $= s(100/\bar{x})$ when $\bar{x}$ is the mean and s is the standard deviation of the sample) of the *Ceraclea ancylus* annual secondary production estimate in Brashears Creek, Spencer Co., Ky., as a function of sample size. C.V. based on 30 replicates per sample size from $n = 1$ to $n = 69$. See text for explanation.

implied that both the interpretation of results and conclusions that are based on an insufficient number of samples may lead to serious errors. Just how many samples *are* sufficient in benthic studies? For the most part, the answer depends on the object of the study. It is apparent that elucidating spatial distribution patterns with dispersion indices generally requires large numbers of samples ($n > 30$, Elliott 1977). But is there a set number of samples that can be taken to estimate the density of an aquatic insect population? This question may best be answered by examining the factors that influence the required number of samples and then relating these to population estimates reported in two previous benthic studies: Needham and Usinger (1956) and Chutter and Noble (1966). These two studies present useful comparisons of the interaction between variability and sample size statistics since the two analyses were done (1) in streams on different continents, (2) using a coarse (Needham and Usinger 1956) and a fine (Chutter and Noble 1966) mesh Surber sampler net (Chutter 1972), and (3) at generic (Needham and Usinger 1956), and mainly specific (Chutter and Noble 1966) taxonomic levels.

Since the number of sampling units required is a function of (1) the size of the mean, (2) the degree of aggregation exhibited by the population, and (3) the desired precision of the mean estimates, several

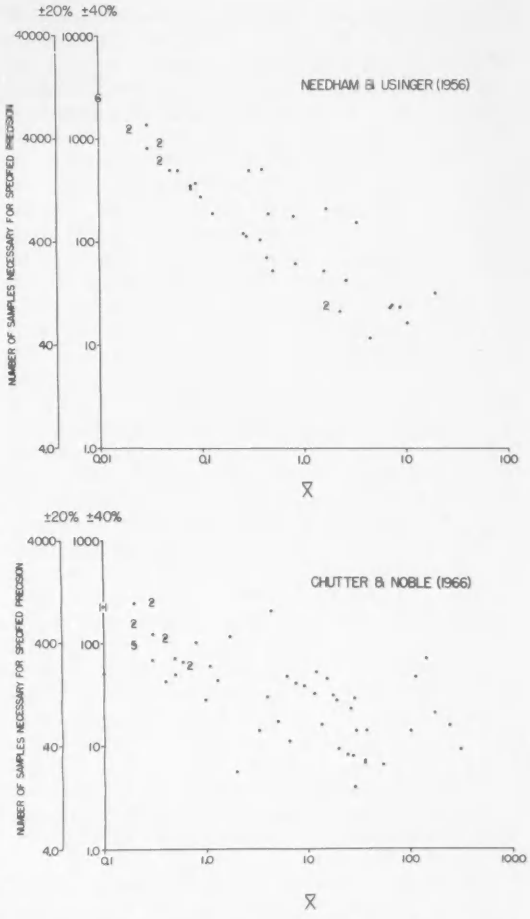
±20% ±40%
NEEDHAM & USINGER (1956)
NUMBER OF SAMPLES NECESSARY FOR SPECIFIED PRECISION
±20% ±40%
CHUTTER & NOBLE (1966)
NUMBER OF SAMPLES NECESSARY FOR SPECIFIED PRECISION

FIG. 7. Required number of samples for estimating mean density at 95% confidence limits ±20% and ±40% of the mean, based on the general formula (Elliott 1977); data from Needham and Usinger (1956, table 3) and Chutter and Noble (1966, table 1). Each point represents a taxon.

conclusions are apparent from reanalyzing the results of these two studies with these three factors in mind (Fig. 7). First, with low population means, greater numbers of samples are generally necessary to estimate mean density than are required with higher means. The relationship between the size of the mean and the required sample size also appears in the following example where sample numbers (for 95% confidence limits ±40% of the sample mean) for data in which the negative binomial distribution serves as a suitable model range as follows (from Elliott 1977, p. 131):

$\bar{x}$	0.5	1	5	10	20	50	∞
n	63	38	18	15	14	13	13

For a mean equal to 0.1 and 0.01 in the above example, 263 and 2513 sample units on which counts are made, respectively, would be needed.

The importance of efficiently sorting benthic samples is obvious here. A major loss of organisms (e.g. from sieving with coarse screens, Mundie 1971) will necessitate data analysis based on lower density counts; assuming that the same degree of aggregation is present, greater numbers of samples will be required for the same precision than would be necessary with more efficient sorting. This factor could be of critical importance in determining whether the densities of two populations are significantly different, a procedure generally requiring large numbers of samples (Cassie 1971; Eberhardt 1978).

Second, it is apparent that the number of required samples varies with the desired degree of precision (Fig. 7). If the tolerable 95% confidence limits are ±20% rather than ±40%, 4 times as many samples must be taken as when the limits were ±40%. The desired degree of precision should be a direct function of the study objectives; it is generally determined by experience or intuition and then modified by cost considerations (Eberhardt 1978).

Third, taxa with similar mean densities may require widely different numbers of samples for the same degree of precision because of differences in population aggregation (Fig. 7). For example, if the negative binomial distribution is a suitable model, the number of samples necessary to obtain an estimate at 95% confidence limits ±40%, calculated by $n = 25(1/\bar{x} + 1/k)$ (Elliott 1977) depends on the value of k. Since k varies with the degree of aggregation, when $k = 0.2$ (assuming the same mean density), 10 times as many samples would be necessary than for when $k = 2.0$ (Elliott 1977).

Finally, Fig. 7 indicates that larger numbers of samples are necessary to accurately estimate density (even at the relatively low precision of ±40%) than are currently being taken in many ecological studies of aquatic insects. This observation will be examined next.

Life History Features and Sampling Variability

How can benthic sampling programs be designed to satisfy statistical considerations (e.g. appropriate degrees of precision), but still be acceptable in terms of the cost and time involved in taking a large number of samples? Two different approaches to this problem will be discussed: habitat stratification and the choice of study populations.

Habitat Stratification

In the designs of previous studies of sampling variability in lotic environments (Needham and Usinger 1956; Allen 1959; Chutter and Noble 1966; Watanabe and Harada 1976; Mason 1976), all samples were collected in a restricted habitat that was generally described as a "uniform" or "near uniform" stream riffle. Thus, sampling conformed to a stratified random rather than a true random design. Although the results of these studies indicated the need for extensive sampling for accurate estimation of population density in an already well-delineated habitat (a uniform stream riffle), several of these studies indicated that variability could be even further reduced by more narrowly defining the sampling area with regard to current (Chutter and Noble 1966), depth (Chutter 1972), or a combination of physical factors (Allen 1959; Mason 1976).

Lamberti and Resh (unpublished data) examined the relationship between substrate composition, spatial distribution patterns, and sampling variability for the limnephilid caddisfly, *Dicosmoecus gilvipes* (Hagen), in a segment of the McCloud River, Shasta Co., Calif. The population of this species in the McCloud River is univoltine with a single cohort and all larvae were active final instars at the time of the study (July 26–28, 1976). The study area was a pool (23 m long, 25 m wide) where substrate had been deposited during periods of maximum discharge to form elevated substrate bars submerged <1 m deep. The substrate rubble in this pool ranged in size from ϕ,3 to ϕ,-5 and included 9 phi scale (Hynes 1970, table I,4) categories. Four substrate ribbons were easily distinguishable within this single pool, three of which had a less variable substrate composition than the fourth (Fig. 8). The spatial patterns of *D. gilvipes* were examined on these four substrate ribbons using counts from Surber sampler collections. Nonaggregated distributions were found on the three ribbons with a less variable substrate composition (Fig. 8, sites 1, 2, and 3; Table 5), whereas an aggregated distribution pattern was found on the ribbon with a broader range of substrate sizes (Fig. 8, site C; Table 5). Consequently, far less effort was required to estimate population density (at a desired precision) using a stratified sampling design for sites 1, 2, or 3 than was necessary for sampling either site C or the entire pool (sites 1–3 + C; Table 5).

The trends observed for *D. gilvipes* in the McCloud River are not unique to either that species or that particular habitat. Similar nonaggregated patterns appeared in the midsummer spatial distribution analysis of benthic chironomids in the uniform silt substrate at 12 m depth in Clear Lake, California (Lamberti and Resh 1977, fig. 1). Other studies, as well, have reported nonaggregated patterns (as random distributions) for benthic populations in relatively uniform substrate (Ricker 1952; Alley and Anderson 1968; and Milbrink et al. 1974).

The interpretation of spatial distribution patterns may be influenced by the dimensions of the sampling unit used. If a population is truly distributed at random, all quadrat sizes should be equally efficient in the estimation of population parameters; however, in nonrandomly distributed populations, quadrat size may in-

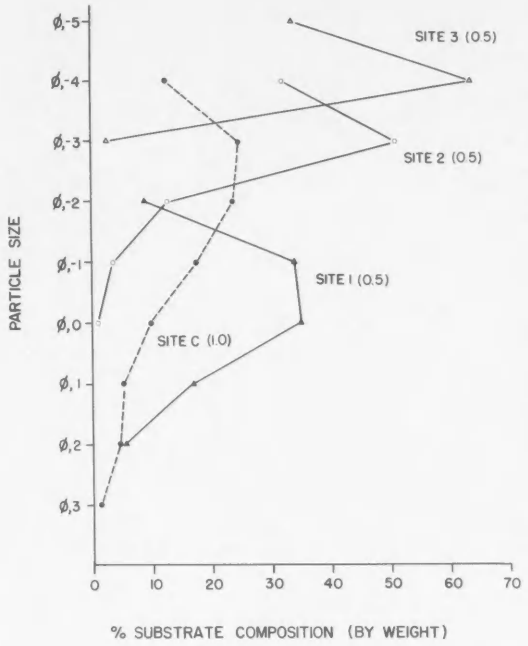

FIG. 8. Percentage substrate composition (by weight as recommended in Cummins 1962) in four elevated substrate areas of a pool in the McCloud River, Shasta Co., Calif., expressed in phi scale units (Hynes 1970, table I,4). Arithmetic quartile deviations (Krumbein 1939) for each site are in parentheses; sorting coefficients (Krumbein 1939): sites 1, 2, and 3 = 1.0; site C = 1.4; sites 1–3+C (corrected for bias due to relative sizes of 1, 2, 3, and C) = 1.7.

fluence the spatial pattern obtained (Elliott 1977). Also, environmental irregularities that affect benthic distribution must be sufficiently large in relation to the dimensions of the sampling unit; the smaller the sample area the finer will be the scale of environmental irregularities that can be detected (Allen 1959). Net-spinning caddisfly larvae, for example, are probably least efficiently studied with a large dimension quadrat such as used in the Surber sampler. In fact, a reduction in sampler dimension may be critical in habitats where the need to collect many samples may obliterate the area under study (Mason 1976). Elliott (1977) and others have pointed out that the smallest sampler dimension possible may be the most appropriate, but oftentimes other factors must be considered (Sugimoto 1969; Holopainen and Sarvala 1975).

The *Dicosmoecus* field study illustrates that sampling variability can be reduced by carefully delineating the sampling sites. Pilot studies using transect sampling techniques along an environmental gradient may indicate differences in variability between habitats. However, when a sampling area is strictly defined, (1) the dimensions of the sampling unit must often be reduced to accommodate the smaller sampling area (and this may change interpretation of the spatial pattern); and (2) extrapolations of population or community dynamics to less restricted habitats become more difficult.

The usefulness of narrowly defining the sampling area to reduce variability is further illustrated in the population and production study of *C. ancylus* (Resh 1977). Data were collected by transect sampling methods that could be subdivided in terms of number of larvae per square metre according to both habitat type (riffle, pool, etc.) and predominant substrate size (ϕ,-6; ϕ,-7; ϕ,-8). In addition, the number of larvae per stone

TABLE 5. Mean number, standard deviation, spatial distribution analysis (maximum-likelihood equation estimation of k, χ^2 test for "goodness of fit," Elliott 1977), and necessary sample sizes for density estimation (calculated using the general formula, Elliott 1977) of *Dicosmoecus gilvipes* (Hagen) on four substrate ribbons (sites 1, 2, 3, and C) and for the entire pool (depth < 1 m, sites 1–3+C) based on counts from Surber sampler collections, McCloud River, Shasta Co., Calif.

	Site 1	Site 2	Site 3	Site C	Sites 1–3+C
$x \pm$ SD	14.5±5.4	3.2±1.9	9.0±3.2	1.3±1.3	6.8±5.9
k	$\rightarrow\infty$	12.2	$\rightarrow\infty$	2.57	1.38
χ^2 test for Poisson (sites 1,2,3) and negative binomial (sites C and 1–3+C) distribution, significance ($\alpha = 0.05$)	$P>0.15$	$P>0.20$	$P>0.35$	$P>0.95$	$P>0.40$
95% confidence limits of mean	Required no. samples				
±10%	56	142	51	400	302
±20%	14	36	13	100	76
±30%	7	16	6	45	34
±40%	4	9	4	25	19

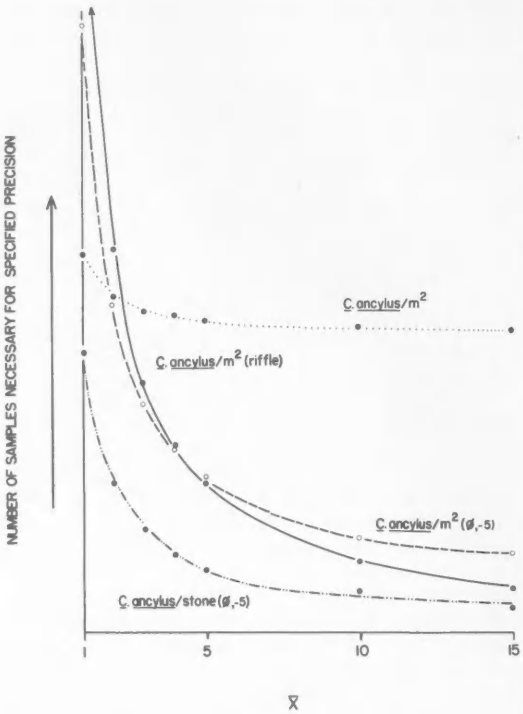

FIG. 9. Required number of samples for stratified (by habitat, substrate type, and individual stone) and unstratified sampling regimes to estimate *Ceraclea ancylus* abundance in Brashears Creek, based on the method of Iwao and Kuno (1968). Units on ordinate axis are a function of desired precision.

(by substrate size) was also recorded (Resh 1977). Using a method devised by Iwao and Kuno (1968) for estimating sample size based on measurements of aggregation through a range of larval densities (Lloyd 1967; Iwao 1968), the relationship between the number of samples necessary for a specified degree of precision and mean density for both unstratified and stratified collections showed that more samples are necessary in sampling the unstratified *C. ancylus* population (larvae per square metre) than when the population is stratified by either habitat (larvae per square metre [riffle]) or substrate type (larvae per square metre [ϕ,-5]) (Fig. 9). The fewest number of samples is required when density is estimated for individual stones (larvae per stone [ϕ,-5]). The individual stone can be considered as the "effective habitat" for *C. ancylus* and has been used as a sampling unit in other studies (e.g. Stout and Vandermeer 1975). In addition to being less variable than the stratified and unstratified quadrats, sampling the "effective habitat" may be the most informative sampling approach in analyzing the population dynamics of *C. ancylus* and other species whose intraspecific interactions occur on an individual substrate unit.

The numbers of samples necessary for estimating population density (Fig. 7) of the abundant taxa in the Needham and Usinger (1956) and Chutter and Noble (1966) studies discussed above are greater than those reported by Mason (1976, table 6) for estimating benthic density at the same level of precision. In the two earlier studies, samples were taken throughout a "uniform" riffle; in Mason's study, the sample size estimates applied only to the midstream area of his study riffle and "three or more times as much effort . . . would be needed to obtain reliable counts riffle wide" (Mason 1976, p. 64). Similar to the *D. gilvipes* and *C. ancylus* examples above, this illustrates the usefulness of carefully stratifying the sampling area to reduce variability.

Choice of Study Populations

Where stratified sampling may provide insufficient data because of the potentially restrictive nature of the sampling design, a more effective approach may be to (1) accept the heterogeneity inherent within the population; (2) correct the variability due to sampling devices (Table 1) and procedures (Table 2) as much as possible; and (3) choose a study organism with sampling characteristics that permit a larger series of samples to be collected and processed with less expenditure of effort, time, and money per sample. For example, in the *C. ancylus* production study many samples could be collected and analyzed with a reduced effort per sample because several features of this species' biology (Resh 1976) were incorporated into the sampling design. First, *C. ancylus* larvae were always found attached directly to the side or underside of submerged stones. Second, *C. ancylus* larvae would only attach to stones that were above a certain size range (ϕ above -3). These two features allowed field separation of larvae from substrate. Third, since the phenology and growth patterns of this population had already been established (Resh 1976), the size range of larvae encountered at each sampling interval was known, and the need to exercise great care in searching for small larvae was only necessary at certain times of the year. Finally, a study area was chosen for the production analysis where substrate could be removed to the level of bedrock, eliminating any possibility of unsampled hyporheic distributions. These features allowed samples to be collected and processed with far less effort than would occur with conventional sampling and sorting programs, thus enabling a large number of samples to be used in elucidating population and production dynamics at the same cost as possible with conventional approaches.

The *D. gilvipes* study is also an example of choosing a population with useful sampling characteristics. First, since this species occurs only on the substrate surface, the possibility of underestimations of density due to an

unsampled hyporheic component of the population was eliminated and the amount of substrate material to be sorted was reduced. Second, the presence of a single instar population eliminated problems due to instar-specific distribution patterns. Third, the large size of the larvae (case length > 3 cm) made them easily distinguishable from the substrate.

In addition to alleviating problems of dispersal and variability in estimating secondary production, knowledge of population phenology can also eliminate the possibility of error due to artificial size-classes in production estimation. For example, Waters and Crawford (1973) speculated that their calculations based on the Hynes–Hamilton method (Hynes and Coleman 1968; Hamilton 1969) may have been an overestimate due to the creation of an artificial size category that resulted in a 10% production increase. However, Resh (1977) reported that this method gave the same production estimate as other widely accepted methods (Ricker 1946, 1968; Allen 1951) when individual larval instars instead of length measurements were used to represent individual size-classes.

The choice of study populations with useful sampling characteristics should not be misconstrued as a mandate to study only "easy" species. Unlike studies in agricultural or forest systems in which the choice of study populations is generally limited to a predetermined pest species, benthic studies rarely have such restrictions. When the analysis of a population with useful sampling characteristics might fulfill study objectives as well as one without these characteristics, failure to choose the "easy" species may result in a sampling design that will generate the same conclusions, but will obtain them at a higher cost and effort than necessary.

Sampling Frequency and Life History Considerations

In many sampling designs, benthic collections are made at regular intervals (e.g. monthly, bimonthly) throughout an annual cycle. Is this regular spacing of sampling intervals the most efficient method for sampling? For example, when the objective of a sampling program is the calculation of secondary production, the use of long, equally spaced intervals provides maximum information about linear decrease, the least frequently encountered type of survivorship curve (Cummins 1975; Waters 1969). In contrast, it provides minimal information for an exponential decrease survivorship curve or other nonlinear, skewed relationships (Waters 1969; Cushman et al. 1978), patterns that are most typical for benthic species (Cummins 1975).

In the schematic presentation of *C. ancylus* survivorship and growth (Fig. 10, based on Resh 1976, 1977), maximum changes in population size occur in the early instars (summer and autumn) and maximum growth occurs in the final instar (spring). These curves resemble those hypothesized by Cummins (1975, fig. 8.2, note calendar differences). Thus, for population analysis, sampling should be more frequent during periods when the population is changing size and structure fastest (e.g. summer for *C. ancylus*, autumn for Cummins' 1975 example).

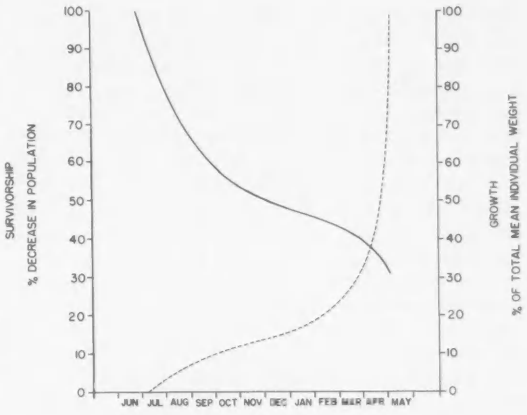

FIG. 10. Survivorship and growth patterns of *C. ancylus* in Brashears Creek based on data reported by Resh (1976, 1977).

However, in production studies the mean individual weight (MIW) for a sampling interval must also be determined. A sampling schedule for exponential growth (see Waters 1969, fig. 2; Cummins 1975, fig. 8.2) that may be appropriate for most aquatic insect population studies (Cummins 1975) may not accurately measure the maximum MIW and consequently may result in an underestimate of secondary production (Resh 1977). Therefore, it may be necessary to make additional qualitative collections to determine maximum MIW (and, as a result, maximum standing stock) and consider correction factors in calculating the annual secondary production estimates. Cushman et al. (1978), using computer simulation techniques, further discusses relationships of sampling frequency and growth curves to secondary production estimates.

Frequency of sampling can also greatly influence the interpretation of results in other types of benthic studies. For example, fluctuations in nocturnal drift patterns may be hidden if sampling periods are longer than 1 h (Elliott 1970). Important fluctuations in chironomid population density can be missed by sampling once a month in contrast to every 10 d (Kajak 1963).

Often, other factors have to be taken into account that may affect sampling frequency and the design of sampling regimes over an annual cycle. For example, spring flooding may limit both accessibility to the study area and the appropriateness of a sampling device that may be effective under certain stream conditions and not others (Table 1B). In addition, during spates populations may undergo drastic changes in spatial distribution (e.g. hyporheic or lateral movements). Density estimates made during these periods may be strongly in-

fluenced by these movements (e.g. see Allen 1959) and decreased density should not automatically be assumed to be the result of mortality. However, sampling during or immediately after extreme events (e.g. drought, spates) may give insights into not only the effect of such events on aquatic biota but also on the factors regulating the colonization and distribution of benthic populations or communities. Ice cover and the intermittent nature of certain streams are examples of other physical features that can influence temporal aspects of sampling design.

The number of samples necessary for a specified degree of precision during one portion of the study organism's life cycle may not apply to another. For example, in the Clear Lake, California study (Lamberti and Resh 1977), nine samples were necessary to produce an estimated mean within 20% of the population mean at 95% confidence limits for *Procladius* spp. during midsummer. In contrast, autumn collections indicated an aggregated distribution pattern and 102 samples would have been necessary for the same degree of precision. Similarly the number of samples necessary for estimating the density of the total chironomid benthos changed from four samples in midsummer to 45 in autumn. This difference in sample sizes was the result of a decrease in population densities and a change from a nonaggregated to an aggregated spatial distribution pattern over time.

If no a priori knowledge about the life history of the study organism is available, it may be best to carry out short interval sampling over periods when the majority of the populations is in the early age-classes, generally late spring through early fall (Cummins 1975). Based on that information sampling frequency can be reduced as appropriate for the study objectives. Future studies of aquatic insects will undoubtedly develop sampling regimes that use a physiological rather than a calendar basis, a technique proven to be effective in studying the dynamics of terrestrial insects (e.g. Hughes 1963; Campbell et al. 1974; Gutierrez et al. 1977).

Final Considerations

In the examples presented in this paper for *Cheumatopsyche pettiti*, *Ceraclea ancylus*, and *D. gilvipes*, the estimation of some population parameter (e.g. density, spatial distribution patterns, secondary production) was the main study objective. In fact, estimations of this type are currently the main focus of benthic research. However, other research approaches may be equally applicable in answering several key questions in benthic ecology. For example, a study to determine whether nonrandom distribution patterns result from physical attributes of the substrate or behavioral properties of the species may be examined by (1) assessing spatial patterns under several different environmental conditions, a sampling–observational approach, or (2) manipulating field conditions or organisms, an experimental–observational approach. Depending on the particular features of this study (e.g. habitat type, study population), the experimental–observational approach may be equally or even more appropriate than the other one. The starting point in developing any study design should be the specification of study objectives. Undoubtedly, some questions in benthic research that are currently under study strictly as estimations of population parameters might be approached better experimentally.

The same three examples and the reexamination of previous studies (e.g. Fig. 7) also suggest that larger numbers of samples are required than are generally taken in benthic studies. In designing field programs, it is possible that far more samples are necessary than time or cost will allow, as is often the case in "one-time only" sampling regimes for environmental impact analysis. In such efforts, rapid assessment techniques requiring minimal field and laboratory efforts (e.g. Cairns et al. 1968; Hilsenhoff 1977) may be preferable to establishing baseline data or drawing conclusions from an inadequate number of samples. Alternatively, habitat stratification and/or judicious choice of study populations may provide sufficient cost reduction to collect the necessary number of samples.

Biomonitoring studies should also consider adopting sequential sampling techniques. Although widely used in terrestrial insect studies (see Pieters 1978), and to a limited extent in marine benthic research (e.g. Saila et al. 1965; Loesch 1974), with rare exceptions (e.g. Sugimoto 1969) this approach has not been applied to freshwater benthic studies. Sequential sampling is most useful in situations where the sorting, identification, and enumeration of sample organisms is more time-consuming than the actual collection of samples (Waters and Resh 1979). This is certainly true in the majority of benthic studies. Along these same lines, incorporation of sampling approaches traditionally limited to other systems (e.g. agricultural or forest environments), or the actual use of sampling devices, extraction procedures, and analysis techniques developed for marine benthic studies (e.g. Holme and McIntyre 1971; Bloom et al. 1977) may lead to greatly improved sampling designs.

In addition to the research needs mentioned above (surface area estimation, sorting procedures, biological influences on sampling design, secondary production estimates), further emphasis is needed in developing methods for analyzing variability in studies of benthic community organization. Variability in numbers of species and individuals collected in a series of benthic samples has been estimated and discussed at length (e.g. Gaufin et al. 1956; Needham and Usinger 1956; Harris 1957; Chutter and Noble 1966; Chutter 1972; Watanabe and Harada 1976; Mason 1976), but the assessment of variability in analysis by diversity indices (e.g. Smith and Grassle 1977) must be considered in far greater detail.

The modeling of the dynamics of freshwater benthos is a relatively new, but rapidly expanding area of research (Cummins 1978). However, the reliability of both new and existing models depends on the validity and precision of the estimated parameter values and on the accuracy of the estimates when applied in field situations (Waters and Resh 1979). That is, are erroneous predictions the fault of the model or of the sampling variability in the field monitoring procedure? This practical aspect of modeling must be given detailed consideration in future studies of this type.

The Ecological Society of America's "Committee on Ecological Life Histories" was dissolved over 20 yr ago after 14 outlines for life history studies had been published. One might hope that the interest generated by this symposium will prompt a renaissance in life history studies of benthic organisms. I do not suggest that we must return to times when such studies were done as an end in themselves, but rather that information obtained from these studies be used to complement advances in sampling methodology and receive maximum consideration in the design of benthic research.

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Sampling Strategies and Life History of Non-Insectan Freshwater Invertebrates[1]

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Life history of benthic freshwater invertebrates, excluding insects, may influence a number of features of sampling programs, such as the environment sampled, sampling technique or equipment used, frequency and timing of sampling, and mesh sizes of nets or sieves. Consideration of the life history should increase the effectiveness of the program and, in the extreme, may allow one to recognize artifacts that would otherwise lead to incorrect conclusions.

Aspects of life history that influence sampling programs are (1) direct or indirect embryonic development and the extent to which young are sampled simultaneously with adults during the breeding season, (2) times of year when various developmental stages are present, (3) differences in size between various life stages necessitating use of more than one sampling method during the year, (4) change in habitat due to migrations or assumption of a pelagic, parasitic, or aerial existence for part of the life cycle, (5) change in mobility over the life cycle, (6) sex differences in size or behavior, and (7) adaptations to adverse conditions. Examples of ways in which life history affects sampling are based on the literature and on original data on the opposum shrimp, *Mysis relicta*, and the crayfish, *Orconectes virilis*.

We recommend that quantitative studies of benthic invertebrate communities be started with a pilot study employing at least two complementary sampling techniques and sufficiently frequent sampling times to allow the development of a reliable strategy for the objective.

Key words: life history, sampling, benthic invertebrates, Crustacea, *Mysis relicta*, *Orconectes virilis*

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Le cycle biologique d'invertébrés dulçaquicoles benthiques, à l'exclusion des insectes, peut influencer plusieurs caractéristiques d'un programme d'échantillonnage, telles que l'environnement échantillonné, les techniques ou les appareils d'échantillonnage, la fréquence et le calen-

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drier de l'échantillonnage et enfin, la grandeur des mailles des filets ou des tamis. En tenant compte du cycle biologique, un programme pourrait être réalisé plus efficacement et, dans des cas extrêmes, on pourrait même reconnaître les artefacts qui, sans cela, auraient conduits à des conclusions inexactes.

Les aspects du cycle biologique qui influent sur les programmes d'échantillonnages sont les suivants: (1) le développement embryonaire direct ou indirect et le degré auquel les jeunes sont échantillonnés en même temps que les adultes pendant la saison de reproduction, (2) les époques de l'année durant lesquelles les divers stades de développement sont présents, (3) les différences de taille entre les divers stades qui rendent nécessaire l'usage de plus d'une méthode d'échantillonnage dans le cours d'une année, (4) le changement d'habitat à la suite de migrations ou de l'adoption d'une existence pélagique, parasitaire ou aérienne durant une partie du cycle biologique, (5) le changement dans la mobilité à un stade ou l'autre du cycle biologique, (6) les différences de taille ou de comportement liées au sexe et (7) les adaptations aux conditions défavorables. Des travaux déjà publiés et des données originales sur la crevette *Mysis relicta* et l'écrevisse *Oronectes virilis* fournissent des exemples de la façon dont le cycle biologique affecte l'échantillonnage.

Nous recommandons de faire précéder les études quantitatives de communautés d'invertébrés benthiques d'une étude-pilote faisant appel à au moins deux méthodes d'échantillonnage complémentaires et un échantillonnage de fréquences suffisamment rapprochées pour permettre l'établissement d'une stratégie fiable en rapport avec l'objectif en vue.

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BENTHIC invertebrates are sampled for a variety of purposes including description of life history or population structure, observation of density and distribution of species and their temporal changes, measurement of secondary production, analysis of community structure, and the study of zoogeography. Sampling programs must, therefore, vary in design in such features as the environment sampled, sampling technique or equipment used, frequency and timing of sampling, and mesh sizes of nets or sieves. In this paper we demonstrate that the life histories of non-insectan freshwater invertebrates may influence any of these aspects of a sampling program. Conversely, failure to consider life history may decrease the effectiveness of the program, the amount of useful information obtained and, in the extreme, may produce artifacts leading to incorrect conclusions.

The majority of benthic invertebrate species are marine. All freshwater metazoan groups appear to have originated from the sea or from the land, with the possible exception of some Turbellaria (Hutchinson 1967). The extensive and useful literature on marine benthos is often ignored in the design of freshwater benthic sampling programs. If the marine experience is to be used to advantage, significant differences in life history between many freshwater invertebrate groups, excluding insects, and their marine relatives (Pennak 1953; Barnes 1974) need to be considered. Some of these differences, which reflect different strategies of evolution in marine and freshwater environments, are as follows: (1) Freshwater species tend to produce fewer and larger eggs per female than do marine forms (e.g. several million eggs by a marine crab compared with 10–800 by a crayfish). (2) The eggs of freshwater species have more yolk than do their marine relatives and thus tend to sink rather than float. (3) Non-insectan freshwater species tend to suppress broadcast fertilization, the individually more valuable eggs being carried or brooded by the parents. Alternatively, the eggs of freshwater species may be attached to the bottom of a lake or stream, whereas marine eggs more often are free-floating. (4) The yolky eggs of non-insectan freshwater invertebrates generally hatch into miniature adults after a period of direct development, whereas in the marine environment free-swimming larval forms, with complete metamorphosis and usually requiring external food, are the rule. The trend in freshwater species toward direct development, suppression of free-swimming larvae, extended parental care, and the release of few but relatively large and well-developed young is nowhere better exemplified than in a comparison of marine bivalves with freshwater clams, the Sphaeriidae. The sphaeriids are hermaphroditic and probably self-fertilize. The inner pairs of gills function as marsupia and an adult may contain from one to 20 young at various stages of development (Barnes 1974). When released, the young are miniature adults, e.g. ~32% as long as the adult in *Sphaerium suecicum* (Clessin) and ~40% as long in *Pisidium crassum* (Jenyns) (Alimov 1970). (5) Unlike most marine invertebrates, freshwater forms can withstand unfavorable environmental conditions by producing resistant stages (resting eggs, cysts, statoblasts, gemmules) or having physiological adaptations to allow adult tissue to tolerate freezing or desiccation.

Relation of Sampling Strategy to Life History

The several features of life history that follow are chosen to demonstrate the need to take into account features of life history when sampling strategies for non-insectan benthic invertebrates are being designed.

DIRECT VS. INDIRECT EMBRYONIC DEVELOPMENT AND DEGREE OF PARENTAL CARE

The extent to which eggs and young are physically

attached to parents during the breeding season and are therefore sampled together with them is important. For example, females of crayfish such as *Orconectes limosus* Rafinesque carry the eggs attached to pleopods during incubation. After hatching, first instars remain physically attached, second instars attach by their chelae, and third instars leave the female intermittently (Crocker and Barr 1968). Thus, a sampling program in which marked adults are captured periodically provides estimates of survivorship of the eggs and first and second instars, but would not be a reliable basis for estimates of survival of the third instars.

All age-classes of the opossum shrimp, *Mysis relicta* Loven, can be sampled by a single method because the eggs are laid into a marsupium where they develop until, at release, the young are $\frac{1}{7}$–$\frac{1}{5}$ the length of the adults. Studies on life history, growth, population dynamics, and energy flow in this species have taken advantage of this characteristic (Lasenby and Langford 1972; Richards et al. 1975; Carpenter et al. 1974).

Young of the leech *Helobdella stagnalis* (L.) also are carried by the parents. Cocoons containing the eggs adhere to the body of the parent. The young, upon hatching, attach by their posterior sucker to the ventral surface of the parent for the first few weeks of life. Thus Davies and Reynoldson (1976) sampled adults, cocoons, and young simultaneously during the breeding season, using either a soft-substrate sampler or collecting by hand for 60-min periods.

Freshwater turbellarians, e.g. *Dugesia polychroa* (Schmidt), attach their few, large yolky eggs to the substrate. Reynoldson (1977) periodically removed all cocoons and adult flatworms from preselected stones in a stream. His 3-wk sampling interval was based on the minimal period of hatching, so that no cocoons would be deposited and hatch between samplings. Breeding period, cocoons per female, eggs per cocoon, and therefore fecundity were readily estimated.

Timing of Reproduction

Timing and frequency of sampling should be related to reproductive periodicity. If the reproductive period is unknown, pilot sampling should be frequent throughout the period when development of young is most likely. To sample the population effectively one wishes to know whether release of eggs or young occurs within a short time or is spread over a long period; whether there is more than one peak per year; whether timing of this release is highly predictable or unpredictable; and whether there is more than one generation per year. In other words, it is necessary to know when the various developmental stages are present if the population is to be sampled effectively.

Change of Size over the Life Cycle

Change in size over the life cycle is implicit, but the difference between adult and young may be large as in crayfish or small as in sphaeriid clams. Large differences over the life cycle may necessitate use of more than one sampling device or mesh size at different times of the year.

Hopkins (1967) sampled the crayfish *Paranephrops planifrons* White in a stream by DC electrofishing. This method sampled most of the population efficiently, except for young-of-the-year. Hand collecting in December showed that many young-of-the-year (stage III, carapace length 3.5 mm) were present, but did not appear in collections by electrofishing until February, when they had molted to stage IV and carapace length was 5 mm. Momot (1967) collected young crayfish, *O. virilis* (Hagen), of <24 mm carapace length by seining the circumference of a Michigan lake with a seine of 0.64-cm mesh. Larger crayfish were captured in baited wire-mesh traps.

Direct collecting with SCUBA gear, although often used as a standard against which to measure the efficiency of other sampling gear, is not necessarily free of bias for the collection of crayfish. Divers may tend to unconsciously select larger animals, particularly if many are escaping simultaneously. Capelli (1975) used a 1–m^2 movable sampling ring to delimit the area in which crayfish (*O. propinquus* Girard) were collected by SCUBA divers, but even so could not adequately obtain young-of-the-year.

Hand collecting of the triclad flatworm *D. polychroa* in an artificial pond was adequate for adults but not for newly hatched young, which were difficult to see. Therefore, during the breeding season Reynoldson (1977) collected the flatworms by baiting, since this attracted all size-groups.

Similarity in size of adults and young occasionally allows one sampling method to collect all ages in proportion to their actual numbers. Alimov (1970) quantitatively sampled sphaeriid populations in Lake Krugloye, USSR, using an undescribed but presumably standard benthic sampling method. Young were released into the population in batches so age-groups were followed through time, and their growth and survivorship and contribution to production and energy flow were readily studied.

Processing grab or other soft bottom samples with an inappropriate mesh size may yield inaccurate data on population size, distribution, migrations, and community structure. Berg (1938) attributed seasonal changes in the depth distribution of larvae of *Chironomus anthracinus* Zett. in Lake Esrom to larval migrations. But, according to Jónasson (1955) the changes in depth distribution of larvae observed by Berg were due to different rates of growth of larvae at various depths to sizes sufficient to be retained by the 0.6-mm mesh used for seiving. In a later study of the same lake, Jónasson (1955) used a sieve with a mesh size of 0.20 mm, and obtained several times more larvae, different depth distributions over the season, and no evidence of migrations. Mesh size must be small enough

to capture the very youngest instar stages for accurate estimates of density. In general, the width and not the length of the animals should determine mesh size. For example, a mesh of 0.6 mm allows chironomid larvae of 10 mm length to pass through.

Jónasson (1955) recognized that an efficient mesh size could change over the season as animals progressed through the life cycle. Tubificid worms passed through the 0.6-mm mesh but this size retained the cocoons. Large tubificids were captured by a 0.51-mm mesh but newly hatched juveniles were captured by 0.26 mm or, more efficiently, by 0.20 mm.

Clearly both the sampler and the method of separating the animals from the sediment must be taken into account when the effectiveness of sampling in soft materials is being judged. It is also essential that investigators report the percent recovery of individuals of each species at various life stages with the mesh sizes used.

Change in Habitat over the Life Cycle

Benthic organisms may not be benthic throughout their life cycle. This necessitates a change in sampling technique or habitat to be sampled.

Several freshwater mites whose life cycles were described by Böttger (1972a, b) are aquatic, benthic, and free-living during part of the life cycle and parasitic on water scorpions, gerrids, hydrometrids, or chironomids during the rest of it. For example, the mite, *Limnesia maculata* (Müller), deposits its eggs in clusters on the substrate or on plants. The larvae run on the substrate until they encounter chironomid pupae. They attach to the pupa until the adult emerges and then they move to the neck of the adult midge where they live as external parasites for 4 d. The engorged larvae then fall off and, if they contact water, pass through one nymphal stage and reach sexual maturity in the benthic environment. Böttger studied aspects of the benthic portion of the life cycle by using an observation box with glass bottom lowered into the water in the littoral zone. Adult chironomids were captured with an aerial light trap.

Unlike the sphaeriids, freshwater mussels (Unionidae) are not benthic throughout the life cycle. They release a free-swimming larva, the glochidium, which, to survive must become attached to the fins or gills of a suitable species of fish. The tissues of the fish encyst the larva within a few hours and the larvae develop for 10–20 d. The mussel then breaks open the cyst and resumes a benthic existence. The large number of embryos (several thousands to a few million per female) can be attributed to the precariousness of the parasitic interval. Benthic samples, of course, miss the glochidium; the host must be sampled for this stage. The host is usually a bottom-dwelling fish that is in the vicinity of the mussels when the glochidia are being discharged (Baker 1928).

Opposum shrimp, *M. relicta*, exhibit both horizontal and vertical changes in habitat during their life cycle. Diurnal migrations to and from the lake bottom are influenced primarily by light intensity and, to a lesser extent, by temperature. During the day, *M. relicta* are on or near the lake bottom; they are farther off the bottom at greater depths or when normal light intensity is reduced by heavy cloud cover (Argyle 1973). Samples from Lake Huron and Michigan during October–November 1971 indicated that juvenile mysids (<10 mm long) were farther off the bottom than adults during the daytime (Table 1). Samples were taken at depths of 55–91 m with four plankton nets (0.656-mm mesh) mounted on a benthic sled (Reynolds and DeGraeve 1972). A 1-m^2 frame was divided into four horizontal strata each with a 0.25×1 m opening; a plankton net was mounted on each opening. On the average, about 97% of all mysids caught were <0.5 m off the bottom and about 50% of those caught were juveniles. Of the remaining 3% caught between 0.5 and 1.0 m off the bottom, almost all were juveniles (Table 1). At night, mysids migrate into surface waters, when the upper strata are cold, but rise only to or near to the metalimnion during periods of pronounced thermal stratification. Juvenile mysids tend to move nearer the lake surface than adults in Lakes Huron and Michigan (Beeton 1960).

Horizontal migrations of *M. relicta* are apparently influenced by reproductive behavior, and they result in seasonal changes in depth distribution of breeding adults and their offspring. During the winter, some adults in Lake Michigan migrate to shallower areas (~25 m depth), where they breed. As water temperature increases during spring, many young are released in these areas. By summer, all surviving mysids have moved lakeward, adults farther than juveniles. In addition, some reproduction takes place continually in deeper waters (70 m depth or more). As a result, length-frequency distributions of mysids sampled in shallower areas consist either of a predominant mode of juveniles or a bimodal distribution of adults and new juveniles. As sampling depth increases, the modes converge and

Table 1. Percentage distributions of *Mysis relicta* captured in a horizontally stratified net mounted on a benthic sled. Samples resulted from nine tows which captured 203 to 19 117 mysids per tow.

Distance above bottom (m)[a]	Mysids in each stratum as % of total captured		Mysids < 10 mm as % of total in stratum	
	Mean	SD	Mean	SD
1.01–1.25	0.7	0.9	99.1	2.8
0.76–1.00	1.0	1.5	97.9	4.4
0.51–0.75	1.6	1.9	55.8	34.5
0.25–0.50	96.7	3.5	52.0	14.9

[a]Includes 0.25 m from the runners to the bottom edge of the nets, which was not sampled.

flatten until, at 70 m and deeper, the population is evenly distributed over the entire length range (Reynolds and DeGraeve 1972).

The results of our horizontal sampling (Table 1) and vertical sampling by N. Grossnickle (Center for Great Lakes Studies, University of Wisconsin–Milwaukee, unpublished data) suggest that vertical tows of a large plankton net at night provide the most representative samples of a population of *M. relicta*. Although vertical tow samples contain smaller numbers of *Mysis* than horizontal ones, the volume of water sampled is more easily quantified. Vertical tows are more representative of the population because they are unaffected by diurnal changes in vertical distribution of *Mysis*. Bias due to changes in horizontal distribution can be reduced by vertical sampling mostly in deeper waters, where population density and length distribution are more stable year round.

Changes in Mobility over the Life Cycle

Samples may be influenced by the mobility of a species throughout its life cycle. Many essentially sessile species possess motile forms for dispersal or reproduction. For example, in sessile rotifers of the suborders Floscullariacea and Collethecacea, young females and males are free-swimming (Hyman 1951) and would be missed by benthic samplers.

Most young of sessile rotifers swim for a short period until they find a suitable substrate, usually a plant, on which to settle. If dislodged, they cannot re-attach. Thus, sampling of plants in shallow waters (Edmondson 1944) could be quantitative for these rotifers. Nevertheless, several exceptional species, e.g. *Ptygura seminatans* Edmondson and *Pseudoecistes rotifer* Stenroos, regularly leave the substrate when disturbed, swim, and then re-attach. These probably would not be sampled quantitatively when plants are collected.

Adult sponges are relatively large and sessile, so the same individual can be repeatedly found. Simpson and Gilbert (1973) have therefore been able to elucidate the timing of egg, sperm, and gemmule production, and also hatching of gemmules in *Spongilla lacustris* (L.) and *Tubella pennsylvanica* Potts. They have described the timing of these events in individuals and in the population. They have also studied development of young *S. lacustris* resulting from sexual reproduction (Simpson and Gilbert 1974). Although they did not sample free-swimming larvae directly, they provided plexiglass slides on which the larvae settled. Growth and development of newly settled individual sponges were then followed for several months. Thus the mobile and sessile stages of sponges were separately used to advantage by these authors.

Newly molted crayfish and egg-bearing females try to remain hidden (Capelli 1975) and are less likely than other stages to be captured even by such direct methods as SCUBA.

The mobility of organisms living in sediments affects their chances of capture by grab or corer. The efficiency of seven devices was assessed against cores taken by a diver. Most were found to be efficient for collecting heavy, buried organisms such as sphaeriids, but there was considerable variation in their ability to capture less dense, surface, or more mobile forms such as oligochaetes and chironomids (Flannagan 1970). This study did not consider life history stages but it noted that some samplers displace water downwards so that their approach is detectable. They may even wash away surface animals. Some devices can be expected to sample disproportionately the heavy or less active life stages or age-classes. The extent of the bias may vary from one device to another.

Artificial substrates are frequently used for studying stream benthos where nonuniform substrates and rapidly flowing water make other methods imprecise (Anderson and Mason 1968). For example, wire basket samplers, filled with stones of uniform surface area and texture and implanted in a stream, are colonized by drifting and crawling organisms. Species compositions and relative abundances can then be used as indicators of environmental perturbation (Mason et al. 1970). Yet some size-classes, such as the young stages are more prone to drift than others (Townsend and Hildrew 1976). Thus, the species and numbers that initially colonize and then remain on a basket sampler can be expected to depend on the nature of the artificial substrate (Benfield et al. 1974), the life histories of the species in the stream, the time of placement of the baskets with respect to life cycles, and on the length of time the substrate is in place.

Loss of organisms upon removal of the artificial substrate from the stream can be an additional source of sampling error (Gale and Thompson 1974). Colonizing organisms such as bryozoans and coelenterates that have become attached are less subject to avoidance behavior or to being shaken off than are active forms such as amphipods and molluscs. Divers can lift the basket samplers into enclosing bags held downstream of the sampler to reduce loss on retrieval (Gale and Thompson 1974; Rabeni and Gibbs 1978).

Dioecism and Differences Between the Sexes in Size or Behavior

Mesh sizes that may adequately sample one sex may have to be of a different size to sample the other. For example, monogont rotifers produce males rhythmically and in response to sudden changes in environmental conditions (Hyman 1951). Some species have males only slightly smaller than females; in others the males may be only $\frac{1}{10}$ the size of the females.

Differences in behavior between the sexes can be an important factor in selecting a sampling technique or in evaluating its limitations. Baited wire minnow traps are widely used to capture crayfish such as *O. virilis*

for scientific or commercial purposes (Threinen 1958; Capelli 1975). Males far outnumber females in the catches by these traps, the percentage of males ranging as high as 99.5 (Threinen 1958; Aiken 1965; Momot 1967; Capelli 1975). Wire traps in Lake 223 of the Experimental Lakes Area, Ontario, during 1976 captured 692 *O. virilis*, of which 86.8% were males and 83% were >41 mm in total length (I. J. Davies, Freshwater Institute, Winnipeg, Man., personal communication). In comparison, he found *O. virilis* ⩾25 mm total length, obtained in the same vicinity by SCUBA, were 52.3% males (95% binomial confidence limits were 40–64%). Capelli (1975) found about a 50:50 sex ratio for *O. propinquus* in Trout Lake, Wisconsin, by SCUBA, although the percentage of males caught by trap varied from 80% to >95%, depending on the season. Capelli suggested that the aggressiveness of large adult males tends to exclude females and smaller males from the traps. Minnow traps used alone are imprecise in determining crayfish population structure or size and sex ratios. Momot (1967) in his study of secondary production of *O. virilis* in West Lost Lake, Michigan, compensated for sex and size bias in the traps by separately calculating the population size represented by each year-class of males and of females from mark and recapture data.

Comparative population estimates of *O. virilis* in Lake 223 show the consequences of trap selectivity (I. J. Davies unpublished data). When Petersen and simple Schnabel estimates based on mark and recapture data from minnow traps were corrected for the sex and size ratios observed independently in the population by SCUBA divers, the estimates were three-fold higher. Additional estimates of population size, made by SCUBA on a stratified areal basis, and by a visual census of marked animals during these areal counts, agreed closely with one another and were about 16 times greater than the corrected Petersen and Schnabel estimates. These data suggest that, in Lake 223, baited wire traps selectively captured large adult males and that a portion of them had a higher probability of being recaptured than others. Thus, bias in the sampling method cannot always be rectified by use of correction factors. An important factor to consider may be the density of traps. Saturation trapping may allow more of the less aggressive individuals to be trapped and so bring population estimates, corrected for trap biases associated with sex and size, closer to the actual population size.

The differential migration of females and males of *O. virilis* that has been reported by Momot (1967) and Momot and Gowing (1972) could be another artifact of sampling crayfish by wire trap. Adult females in Michigan lakes apparently started migrating to deeper waters in July and August. Males and yearlings migrated later in the season. The female migration was thought to be associated with gonadal maturation, which requires low temperature and darkness (Momot and Gowing 1972). Alternatively, aggressive behavior of the adult males forces the females out of preferred shallow water areas into deeper waters (Fast and Momot 1973). Capelli (1975), using SCUBA, reported downward migrations of larger adults of *O. propinquus* in the early fall but no difference in movement between females and males. I. J. Davies (unpublished data), using SCUBA, did not observe differences in depth distribution or migration patterns of female and male *O. virilis* in Lake 223. Capelli (1975) reported that the proportion of female *O. propinquus* in the traps was highest in July and early August, following release of the young. The data obtained by using wire traps may therefore indicate the relative susceptibility to trapping of crayfish depending on their size, sex and breeding state, rather than reflect primarily the density of individuals. Apparent differences in distribution of the sexes as crayfish move to deeper water in late summer and fall could be the outcome of less male aggression in colder, deeper water, so that more females are trapped there.

Sampling Invertebrates Adapted to Adverse Conditions

Invertebrates produce a variety of dormant or resistant stages such as gemmules, cysts, and statoblasts or may have physiological adaptations that allow the functional, adult tissues to withstand the extremes of temperature and water level in temperate freshwater habitats. The survival of functional tissue during adverse conditions is an important consideration in estimating annual production. *Spongilla lacustris* asexually produces gemmules in fall, as overwintering structures that are capable of regenerating a whole animal the following spring (Simpson and Gilbert 1973). No functional tissue (that possessing canals, flagellated chambers, and mesenchyme) survives the winter in colder localities, and annual secondary production can be rather readily measured from standing crop estimates obtained over the spring and summer, providing loss due to grazing is low. Consideration must be given, however, to the fact that only the living biomass is produced annually. The skeletal portion lasts from year to year (Gilbert 1975). In other localities, there is evidence that some members of this species overwinter as functional tissue. Sponges produced from gemmules that hatch very late in the season do not gemmulate at the normal time in the fall (Gilbert 1975). Clearly, sampling during the winter is necessary to establish what proportion, if any, of the functional tissue survives under the ice. Further, species are known that do not produce gemmules (Simpson and Gilbert 1974; Gilbert and Hadžišče 1975). It is important for production estimates to know if a species is annual or perennial, and, until this is resolved, the population must be sampled year round.

Monogont rotifers produce thick-walled resting eggs

under freezing or drying conditions, the presence of which could complicate production estimates. Gilbert (1974) noted that the resting egg pool of a natural population probably contains eggs produced at different times of the year during different years, and under different environmental conditions. Even eggs produced during the same sexual period may hatch after varying lengths of time and under a range of environmental conditions. Population numbers at any one time may thus be influenced by the rate of parthenogenetic reproduction as well as by the rate of hatching of eggs produced at varying times in the past.

Discussion

One consequence of inadequate quantitative sampling is seen in the use of diversity indices. Diversity indices that measure species evenness, for example, Simpson's or the information measures such as H or H′ (Pielou 1969) depend on knowing the number of individuals of each species. A lowering of the index of diversity is used as a measure of the impact of an environmental change on benthic communities (Wilhm and Dorris 1968; Hendricks et al. 1974). Therefore, care must be taken to ensure that an observed change in numbers is not a normal consequence of the life history of a species (e.g. increases at reproduction) or, alternatively, of an inefficient sampling method (e.g. underestimation due to a large mesh size). Many contemporary studies of community diversity, unfortunately, neglect to consider variations in sampling efficiency throughout the life cycle of the species.

The fact that a species passes through a series of developmental stages with time rather than being a static entity is a fundamental concept to biologists. Yet most reviews and manuals of benthic sampling (e.g. Edmondson and Winberg 1971; Holme and McIntyre 1971; Hulings and Gray 1971; Brinkhurst 1974) do not emphasize life history when a sampling program is being planned. Most studies on single species have considered life history (cf. examples above). Many studies of invertebrate communities, on the other hand, largely ignore life history and are based on samples taken at arbitrary time intervals with only one type of gear. We recommend that a quantitative community study begin with a pilot study employing at least two complementary sampling techniques and having sufficiently frequent sampling times to allow a reliable strategy to be developed for the chosen objective.

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Contribution of Life History Information to Taxonomy of Aquatic Insects[1]

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OLIVER, D. R. 1979. Contribution of life history information to taxonomy of aquatic insects. J. Fish. Res. Board Can. 36: 318–321.

Life history studies may contribute to taxonomy by providing corroborative or clarifying data about existing taxonomic systems or may suggest reevaluation. Specifically, life history studies may provide information on the presence or absence of reproductive isolation, asso-

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ciated life stages, monospecific specimens, specimens for character evaluation, and a forum where ecologists and taxonomists may interact.

Key words: taxonomy, life histories, benthos, reproductive isolation, life stages, character evaluation

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Les études de cycle biologique peuvent contribuer à la taxonomie en fournissant des données susceptibles de corroborer ou de clarifier les actuels systèmes taxonomiques, ou encore suggérer une réévaluation. Plus particulièrement, les études de ce genre peuvent nous éclairer sur la présence ou l'absence d'isolement reproducteur, sur les stades biologiques associés, des spécimens monospécifiques, des spécimens qui serviront à l'évaluation des caractéristiques et enfin une tribune où écologistes et taxonomistes peuvent échanger des idées.

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TAXONOMY, by its very nature, is ad hoc. A decision has to be made about the identity and status of a group of organisms using available data. These decisions are subject to continual revision and reassessment as further information becomes available. Successive application of more and more data of various types usually will increasingly clarify knowledge about taxon limits. This paper briefly considers how data derived from the ecological study of life histories can contribute to the taxonomy of aquatic insects.

Events that govern the reproduction (and survival) of a species or a population are termed life history. Life history may be described by fecundity, development, and longevity, and may include behavioral aspects (habitat selection, mating, shelter construction, feeding, etc.) that affect these parameters.

Species are complex biological systems and definition of their boundaries ultimately depend upon demonstration of reproductive isolation between them. Application of the biological species concept as defined by Mayr (1969) — "groups of actually (or potentially) interbreeding populations which are reproductively isolated from such other groups" — is often difficult for a taxonomist. Frequently, taxonomists have little or no biological information about the specimens they study and so infer reproductive isolation from discontinuities in taxonomic characters. Discontinuities, however, may be due to other reasons (e.g. polymorphism). Similarly, although discrete groups of specimens can be recognized and defined by taxonomists, the taxonomic status of these groups remains uncertain.

Several examples follow that illustrate how non-morphological information obtained through life history studies can determine the presence or absence of reproductive isolation and thereby contribute to clarification of taxon limits.

Reproductive Isolation

Edwards (1926) recognized two varieties of the ceratopogonid *Culicoides pulicaris* Meigen: *pulicaris* and *punctatus*. Based on new morphological data augmented by life history information, Downes and Kettle (1952) elevated these varieties to specific rank. All life stages are morphologically similar; male genitalia are identical. Except for a few intermediate specimens the adults could be assigned to one of the two varieties by wing markings, thoracic color, and size. The larvae were always distinguishable by head capsule size. The two varieties are frequently sympatric and synchronous, the very situation on which Downes and Kettle based their study. They found the larvae were segregated, probably due to selective oviposition by females. Males swarmed at the same time in the same place but the swarms of the two forms remained separate. Thus when the two forms occurred together, interbreeding did not occur due to behavioral differences and so the two varieties were regarded as distinct species. Although Downes and Kettle (1952) demonstrated morphological differences in the larvae, they probably would not have assigned specific status to the varieties of *C. pulicaris* without corroborative life history information.

The widely distributed house mosquito, *Culex pipiens* Linnaeus, has a number of morphological and ecological variants (biotypes) throughout its range (Mattingly 1957). Some of these variants are autogenous, others are anautogenous. Some overwinter in the egg stage, others as adults. Furthermore, there are a number of more or less incompatible breeding types with morphological differences. Seventeen reproductively differentiated forms have been recognized in breeding experiments (Downes 1973). The taxonomic status of the various populations of *C. pipiens* is a complex problem and the results of Spielman's (1964) investigation of two sympatric populations is a significant contribution. He studied autogenous and anautogenous populations living together in utility tunnels under buildings. In the laboratory, the two forms readily interbred and produced fertile progeny. In nature, females were homozygous for either autogeny or anautogeny; $<3\%$

were heterozygotes. He observed that the autogenous type did not overwinter as females and that they mated near the larval habitat, whereas the anautogenous type overwintered as females and mated away from the larval habitat. When adverse weather conditions prevented the spread of anautogenous females, interbreeding occurred near the larval habitat between the two populations. Spielman (1964) concluded that the two types did not, normally, freely interbreed when they occurred together but since interbreeding did occur, albeit rarely, the two variants of *C. pipiens* should not be considered different species.

Mating behavior was used in the above studies to determine the presence or absence of reproductive isolation. Similarly, based on a study of stridulation, Jansson (1972) reduced the number of species in the hemipteran genus *Cenocorixa* from 13 to 8. Other types of life history information also may be used to corroborate inferences about reproductive isolation. For example, Angus (1973) found differences in emergence times and flight activity among several species of the beetle genus *Helophorus* whose taxonomic status had been questioned. He also found specific differences in larval morphology and egg cocoons. Sawchyn and Gillott (1974) distinguished two species of damsel-flies in the genus *Lestes* by incision patterns in plant stems and by the number of eggs inserted.

Some morphological differences existed among the species discussed thus far (except perhaps between the variants of *Culex pipiens*), however, reproductive isolation of conspecific individuals from closely related species is not always accompanied by morphological distinctness. There was no morphological difference between intertidal and sublittoral populations of a marine Chironomid, *Clunio*, living in the same area (Heimbach 1978). Mating between individuals of the two populations occurred in the laboratory but complete reproductive isolation existed in nature due to differences in time of eclosion, mating, and oviposition. Heimbach (1978) concluded that the two populations belonged to different species and described a new species based solely on these biological differences. Similarly, Oliver (1976) was unable to demonstrate morphological differences between a parthenogenetic chironomid, *Lauterbornia sedna* (Oliver), and a related bisexual species, *L. coracina* Kieffer. Based on morphology, both Heimbach (1978) and Oliver (1976) could have assigned their new species to a previously described species but this would have ignored the fact that they were biologically distinct.

Use of life history information alone in distinguishing species can be a bane to the taxonomist who relies solely on morphological characters of dead specimens. The absence of morphological differences may require that specimens be assigned only to species groups. Demonstration of reproductive isolation should induce a taxonomist to search for new characters, a search that will probably succeed.

Finally, it should be noted that verification of reproductive isolation among species can also be used to corroborate previously defined taxon limits.

Life Stages

Knowledge that certain immature stages and adults belong to the same species aids in the search for distinguishing taxonomic characters in one or all of the life stages. For example, the adults of two trichopterans, *Ceraclea maculata* (Banks) and *C. spongillovorax* (Resh), based on morphological characters, could be considered a single species (Resh 1976). Investigation of the immature stages revealed differences in the morphology of the larvae and pupae, and in feeding. *Ceraclea maculata* feeds on detritus and *C. spongillovorax* on sponges. By rearing individual larvae, "identified" adults of both species were obtained and study of these led to recognition of characters for species discrimination. Resh (1976) concluded: "If the ecology and morphology of the immature stages of these two species had not been known, the cryptic adult stages of *C. spongillovorax*, would probably have remained undescribed."

Similarly, evidence that specimens of the same life stage come from sympatric but reproductively isolated populations provides an initial grouping that may be used in the search for taxonomic characters. Lindeberg (1964, 1967) used this type of information to obtain specimens of several closely related species of chironomids belonging to the genus *Tanytarsus*. He observed that adult *Tanytarsus* in a given area occurred in discrete, monospecific swarms. By collecting and analyzing "pure" samples of specimens from these monospecific swarms he was able to define morphological characters for species recognition. He was perhaps made aware of this approach by an earlier study (Lindeberg 1963) which led him to split *Tanytarsus brundini* Lindeberg from *T. curticornis* Kieffer. Although division into two species was possible on morphological characters alone, his decision was supported by corroborative evidence provided by discrete swarming.

Cooperation Between Taxonomists and Ecologists

A taxonomist alone may obtain and use life history information to augment taxonomic studies but it would be more efficient if taxonomists and ecologists would exchange information during the course of a study. For example, I identified samples of a chironomid from Fort Simpson, Northwest Territories, as *Cricotopus bicinctus* (Meigen). I was confident of this identification as only the larvae of *C. bicinctus*, among *Cricotopus*, had spines on the inner margin of the mandible. However, during a life history study, Rosenberg et al. (1977) found two discrete head capsule sizes in third and fourth instar larvae. Was the cause due to size differences between sexes, which has been ob-

served in fourth instars of other species, or due to two closely related species living sympatrically? A reexamination of specimens, including reared-associated material, resulted in the recognition of a new species, *C. mackenziensis* Oliver (Oliver 1977), separable in all stages from *C. bicinctus*. It should be noted that the larvae of both species have mandibles with spines on the inner margin. Generally, taxonomists will not look further if they are able to identify specimens by one or two characters they believe to be diagnostic for a species unless prompted by additional, contrary evidence. I have obtained this additional evidence working with ecologists and, although not explicitly stated, it has led to the description of several new species (Oliver 1971, 1976). A life history study is one area where ecologists and taxonomists may interact and enter into a dialogue that will contribute to each discipline.

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Use of Macroinvertebrate Life History Information in Toxicity Tests[1]

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Life history information of macroinvertebrates is an important variable to consider when interpreting the results of toxicity tests. The importance of life history information has been recognized in the culturing of macroinvertebrates, but only in the last 5 yr has emphasis been placed on using this information in the design of acute and chronic toxicity tests. Sensitivity of organisms to toxicants is affected by nutrition, physiological requirements, behavior, predator–prey interactions, substrate, current, and light. There is need to integrate these, and other

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variables, to produce more defensible tests. Some features of life history may be used as end points in tests.

Key words: macroinvertebrates, life history, toxicity, tests, design, sensitivity

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Les données relatives au cycle biologique des macro-invertébrés constituent une importante variable à prendre en considération lorsqu'il s'agit d'interpréter les résultats des contrôles de la toxicité. La valeur de cette information a été reconnue dans le cadre de la culture des macro-invertébrés, mais c'est seulement au cours des cinq dernières années qu'on s'est penché sur son utilisation pour la conception des contrôles de la toxicité aiguë et chronique. La sensibilité des organismes aux substances toxiques subit l'influence de la nutrition, des exigences physiologiques, du comportement, des interactions prédateur-proie, du substrat, du courant et de la lumière. Il faut intégrer ces données et d'autres variables afin de produire des contrôles plus justifiables. Certains traits du cycle biologique peuvent servir de points déterminants dans les contrôles.

IN the United States in 1977, the National Resources Defense Council sued the Administrator of the Environmental Protection Agency for noncompliance with Section 304 of Public Law 92-500. Briefly, the Administrator was charged to ". . .develop and publish . . . criteria for water quality accurately reflecting the latest scientific knowledge (A) on the kind and extent of all identifiable effects on health and welfare . . .; (B) on the concentration and dispersal of pollutants or their byproducts . . . , and (C) on the effects of pollutants on biological community diversity, productivity, and stability . . . ." Further, the Administrator was charged to "Develop and publish . . . information (A) on the factors necessary to restore and maintain the chemical, physical, and biological integrity of all . . . waters . . .; (B) on the factors necessary for the protection and propagation of shellfish, fish, and wildlife . . .; and (C) on the measurement and classification of water quality . . ." As a result of this suit, 65 chemicals and classes of chemicals were identified as hazardous to aquatic life and man (Quarles 1978). In response to this suit, EPA issued 65 draft criterion documents that reviewed the literature and attempted to arrive at scientifically justifiable water quality criteria for protecting aquatic life and man.

Unfortunately, the paucity of published toxicity data made it difficult to establish criteria for many chemicals or classes of chemicals. Further, the state of the art is such that safe concentrations for many toxicants in the environment can only be determined by multiplying LC50 values by application factors (NAS/NAE 1973). Ideally, safe concentrations of toxicants should be empirically derived from MATC (maximum allowable toxicant concentration) values obtained by conducting chronic or subchronic studies on aquatic organisms. A review of the toxicity literature indicates that only a few chronic or subchronic studies have been conducted on toxicants and those studies are limited to very few aquatic species (Sprague 1976).

The question can be asked, "Why are so much of our toxicity data unusable for setting water quality criteria?" One reason is that most toxicity studies, while conducted with the best scientific information available, are woefully inadequate because life history information was not incorporated into the experimental design and data interpretation. This conclusion is especially applicable in the case of acute toxicity tests because simple lethality data conducted with "standard" toxicity tests are intrinsically difficult to interpret and even more difficult to extrapolate to field conditions. Deficiencies in life history information are particularly conspicuous in cases where discharge permits require toxicity testing with indigenous species about which little is known in terms of life history.

The purpose of this paper is to address the importance of life history information in conducting toxicity tests with macroinvertebrates. Topics covered include a review of the trends in conducting toxicity tests over the past 10–15 yr, a discussion of important life history variables that may affect toxicity test results, and an overview of future informational needs regarding the relationship of life history information to macroinvertebrate toxicity tests.

Definitions

At the outset, it seems necessary to distinguish between the terms "life cycle" and "life history" and their application to toxicity tests. The literature abounds with references to life cycle and life history and the terms appear to be used interchangeably and indiscriminately.

For the purpose of discussion, we define the terms as follows:

Life Cycle: a series of stages in form and function through which an organism passes between the successive recurrences of a specified primary stage (e.g. egg to egg).

Life History: a series of changes through which an organism passes in its development from the primary stage until its natural death. Implicit in this definition is that "history" refers to a multifactorial consideration of all parameters that impinge upon an organism during its life. These parameters include life cycle information (including physiology and genetics), predator–prey interactions, competition, physical–chemical parameters, resource interactions, and behavior.

Two additional terms often applied to toxicity tests should be distinguished: rearing and holding. Rearing is applied when gravid females are brought into the laboratory and the offspring are used in toxicity tests. Holding applies when various life stages are brought into the laboratory and briefly held before they are used in tests. In both practices, use is made of specific life cycle stages of the subject species; however, neither practice really incorporates life history information.

Historical Perspective

A review of about 100 macroinvertebrate toxicity papers published in the last 10–15 yr demonstrates that about 50% of the studies incorporated neither life history nor life cycle information in the experimental design. Most were simple acute lethality tests conducted with field collected specimens that were not properly acclimated to test conditions nor described as to size, age, sex, condition, or species. Further, many were static tests conducted with no toxicant renewal or aeration and were conducted under "standardized" conditions which usually included a glass beaker, pickle jar, or aquarium. Apparently the state of the art was such that life history information was not considered to be very important in generating toxicity data.

Approximately 45% of the papers published since 1965 incorporate some life history information in toxicity testing and most of these papers were published in the last 5 yr, a time period that coincides with the passage of Public Law 92-500.

The use of life history information in toxicity testing probably became important for the following reasons:

1. A need to establish cultures so that massive numbers of animals were available for acute toxicity tests.
2. A need for test animals of known age or life stage so that sensitivity of the organism to toxicants could be maximized.
3. A need to conduct chronic and subchronic tests so that empirical MATCs could be derived, and survival of control organisms be ensured.
4. A natural curiosity to explain why field populations of macroinvertebrates were killed or redistributed in their habitats.

Use of Life History Information in Toxicity Tests

We acknowledge that it would be impossible to design a toxicity test that incorporates all aspects of life history. However, we are concerned that many current toxicity tests only use elementary life history information in their design. The reason for this concern is obvious: if attempts are not made to incorporate life history information into toxicity tests, we will probably continue to obtain test results that may be dependent on the test conditions rather than the toxicant.

In this section of the paper, examples are discussed where life history information has been, could be, or should be, used in toxicity test design. There is no attempt to distinguish between acute and chronic tests and only pertinent literature is cited.

Culturing

Standard Methods (APHA 1976), the EPA documents on acute toxicity tests (EPA 1975, 1978), and the American Society of Testing and Materials (ASTM) draft documents suggest over 165 aquatic species for toxicity tests. Of the suggested species, only 40 are freshwater macroinvertebrates and <15 have been cultured in the laboratory. Among these 15 species, only 4 invertebrate groups are represented: Amphipoda, Malacostraca, Ephemeroptera, and Diptera. Notably absent from the published lists are culturable species that have been used in toxicity testing; these include gastropods (Wurtz and Bridges 1961; Cairns and Messenger 1974), bivalves (Chandler and Marking 1975; Paparo and Sparks 1977), triclads (Llewellyn 1973; See 1976), oligochaetes (Newman 1975), and rotifers (Schaefer and Pipes 1973; Bunting and Robertson 1975; Buikema et al. 1974a, b, 1977).

The apparent reluctance to widen the range of macroinvertebrates used in toxicity testing may simply be related to the fact that ecological information on many species is lacking and, consequently, those species cannot be cultured or even maintained in the laboratory. Secondly, because there is a conscious effort to obtain data rapidly, macroinvertebrates with longer field life cycles have been largely ignored. Long generation time should not *a priori* preclude a species from being considered as a candidate test animal. With adequate life history information, it may be possible to shorten generation time as was accomplished in the case of the grass shrimp, *Palaemonetes pugio*, whose cycle was shortened from 12 to 3 mo by controlling photoperiod and temperature (Little 1968).

Until more importance is attached to field data and more emphasis placed on culturing and chronic toxicity tests, most toxicity data will be restricted to a few taxa. Consequently, water quality criteria also will be based on limited data and more appropriate sensitive species may never be recognized.

Life Cycle Information

Standard Methods (APHA 1976), the EPA documents on acute toxicity testing (EPA 1975, 1978), and ASTM draft documents discuss the need to use sen-

sitive life stages in toxicity tests. Sensitive life stage usually refers to immatures, molting stages for Crustacea and insects, and to ovigerous females. That immature animals are generally more sensitive to toxicants has been documented for many macroinvertebrates including crayfish (Hubschman 1965; Heit and Fingerman 1977), insects (Clubb et al. 1975a; Maki et al. 1975), and snails (Wier and Walter 1976; Harman 1974). Immature animals are more sensitive for a variety of reasons including (a) they have larger surface:volume ratios and therefore have more exchange with the environment; (b) they may have a higher initial lipid content, thus increasing the uptake of lipid soluble toxicants; (c) they have a higher weight specific metabolism which could facilitate uptake of toxicants; and (d) in the case of arthropods, they molt frequently during the early developmental periods.

Molting has long been recognized as a sensitive period to toxicant and natural stresses. The principal reason for this increased sensitivity is the rapid and nonselective influx of water and toxicant during molting (Lee 1976). Elder and Gaufin (1974), working on the sensitivity of the stonefly *Pteronarcys* to mercury, suggested that the catabolic processes occurring during molting also may affect organism sensitivity to selected toxicants.

Increased sensitivity of ovigerous female amphipods to toxicants is probably related to the increased metabolism during oogenesis and brooding, and the increased lipid mobilization and synthesis (Emery 1970). Sensitivity to lipid soluble compounds would definitely be increased during this period.

Differential responses can occur between sexes. This has been demonstrated for crayfish but the pattern was masked by size differences (Heit and Fingerman 1977); generally females survived best.

Reproduction

By definition, reproduction fits into both life cycle and life history. Reproductive impairment is a good measure of stress because reproduction is a product of all factors that have affected metabolism (feeding rates, assimilation efficiencies, energy expenditure for biochemical processes, behavior, etc.). Obtaining reproductive information requires the ability to satisfactorily culture animals in the laboratory and to reduce reproductive variability within controls and various test conditions. Reproductive data have been obtained for sexual forms such as snails (Flannagan 1974) and amphipods (Nebeker and Puglishi 1974; Arthur et al. 1974; Arthur and Eaton 1971; Oseid and Smith 1974a; and Macek et al. 1976a, b). Asexual forms such as the oligochaete *Aeolosoma* (Newman 1975) and the triclad *Polycelis* (Kouyoumjian and Uglow 1974) have also been studied. On the evidence of reproductive impairment empirical MATC's have been described for several toxicants (e.g. Macek et al. 1976a).

Newman's work (1975) was interesting because the concentration of zinc that stimulated reproduction was close to an average surface–water zinc concentration. Also, his research demonstrated that zinc stress inhibited scissiparity (pygidial budding) of subsequent zooids and that the type of scissiparity could be shifted from paratomy (cephalic region developed before splitting) to architomy (no cephalic region developed before splitting), a criterion used in the taxonomy of *Aeolosoma*.

Physiology

Like reproduction, physiological responses overlap with life cycle studies and for that reason molting was discussed above. Toxicant effects on oxygen consumption (e.g. Zimakowska 1973; Sheanon and Trama 1972) have been studied, and Clubb et al. (1975b) concluded that metal uptake by aquatic insects was related to increased metabolic levels. Uptake and depuration studies are quite common (e.g. Kawatski and Bittner 1975; Renzoni and Bacci 1976) and the effects of toxicants on water balance in snails has been examined for *Biomphalaria* (Cocks 1973) and *Lymnaea* (Spronk et al. 1971). Effects of pesticide on growth of *Chironomus tentans* was investigated by Macek et al. (1976a, b), and Thornton and Wilhm (1974) evaluated effects of pH, phenol, and sodium chloride on caloric values and nitrogen and lipid levels of *C. attenatus*. Using a comparative physiology technique, Paparo and Sparks (1977) proposed the use of ciliary beat rate of the fingernail clam (*Musculium*) to assess water quality.

Research incorporating previous life history information of field collected test organisms in the experimental design is rare. Albaugh (1972) showed that crayfish collected from an area sprayed with pesticide were more tolerant to pesticides than were crayfish evaluated from cleaner areas. Cairns and Sheier (1957) showed that physids acclimated to low oxygen concentrations were more tolerant of combined toxicant–oxygen stress than were nonacclimated snails.

Physiological studies on aquatic organisms are valuable for evaluating mechanisms of toxicant action; however, Sprague (1976) points out that physiological tests "have yielded disappointingly few criteria." We agree with his reasoning that "there is more interest in unraveling the intricacies of a particular physiological discipline, than in providing water quality criteria."

Nutrition

Using the "macroinvertebrate" *Daphnia*, Buikema et al. (1979), Winner et al. (1977), and others have shown that food quality affects the organism's sensitivity to toxicants. Food availability also affects invertebrate behavior (Siesennop 1972; Wallace et al. 1975). These two aspects of food, quality and availability, are important variables that should be con-

sidered in conducting toxicity tests. A poorly fed or unfed organism is prestressed before being exposed to a toxicant, and resultant data may be spurious. Further, an invertebrate that expends considerable energy "searching" for food may be more sensitive to certain classes of toxicants because of its higher metabolic rate.

Predator–Prey Interactions

Predator–prey interactions have not been widely used in toxicity tests although some toxicity data have been interpreted as increasing an organism's susceptibility to predation (e.g. Fremling 1975). Predation, which is a significant factor in most invertebrate populations, could be increased if the animals behaved abnormally, e.g. failing to be negatively phototactic or rheotactic. Sherberger et al. (1977) studied the effect of thermal shock on drifting insects. One variable they tested was whether thermally stressed mayfly nymphs (*Isonychia*) would be more susceptible to predation by the banded sculpin, *Cottus carolinae*. While their conclusions were negative, their approach should be considered as unique and worthy of more research.

Behavior

Many of the variables discussed above relate to modification of behavior that could affect an organism's sensitivity to toxicants. However, the converse also needs to be discussed, i.e. behavior modification as an indicator of stress and a predictive endpoint in toxicity tests. Until behavior studies are conducted and careful observations are made, the use of behavior as an analytical toxicity tool for macroinvertebrates will not proceed as rapidly as it has for fish (e.g. Cairns and Westlake 1975). Maciorowski (1978) designed a preference–avoidance behavior study of crayfish exposed to toxicants. See (1976) evaluated the efficacy of planarian crawling speed and Kouyoumjian and Uglow (1974) studied the flip-over response of *Planaria*. Maki et al. (1973) discussed ventilation rates of hellgrammites and push-up responses of plecopterans in response to toxicant stress. Sherberger et al. (1977) examined thermal shock effects on rheotactic and phototactic responses of *Isonychia* and Anderson et al. (1976) studied the shell closing response of *Corbicula*. While the results of many of these studies were negative or inconclusive, the potential for using behavior as an analytical tool in toxicity tests is good.

Physical–Chemical Parameters

The major physical–chemical parameters that affect macroinvertebrate distribution and abundance in the field also have been identified as parameters that affect their sensitivity to toxicants. A brief review of the importance of these parameters follows.

Substrate requirements for macroinvertebrates have been recognized for some time (see discussion in Hynes 1970). Absence of substrate increased the level of amphipod activity (Wallace et al. 1975), and Oseid and Smith (1974b) and Eriksen (1963a) demonstrated that organisms that did not have an adequate substrate were more susceptible to toxicant stress. Fremling (1975) provided an artificial substrate for *Hexagenia* to satisfy their thigmotactic response and to reduce fatigue associated "with searching for a substrate." Similarly, substrates were provided for mayflies and plecopterans in acute toxicity studies by Nebeker and Lemke (1968), Bell and Nebeker (1969), and Gregg (1974) so that the organisms could orient to current. Substrates have been used more frequently as interest developed in chronic and subchronic studies and culturing of test animals. Substrates are routinely used in long-term studies involving amphipods (e.g. Arthur and Eaton 1971; Arthur et al. 1974) and chironomids (e.g. Macek et al. 1976a).

Test vessel size and shape, although not aspects of substrate, are identifiable physical variables that also affect sensitivity to toxicants and may need to be considered (Eriksen 1963b; Oseid and Smith 1974b). The major consideration here is one of sufficient room to avoid crowding.

Current is well documented in the literature as a significant variable affecting the distribution, abundance, and behavior of organisms. Even though it is well known that many macroinvertebrates require current for survival (e.g. Knight and Gaufin (1963) found that nymphal stages of *Acroneuria* (Plecoptera) rely on current to irrigate their gills), current has rarely been incorporated into toxicity test design. Most toxicity tests are static and often, therefore, produce indefensible data because behavioral and physiological requirements for current by specific organisms are ignored. Current has been largely ignored in most continuous flow bioassay designs where the water flow is used to maintain constant toxicant levels rather than to provide an appropriate current for test organisms. Exceptions include Surber and Thatcher (1963), Nebeker and Lemke (1968), and Gregg (1974).

Light quantity and quality affect both behavior and physiological cycles of organisms and therefore probably also affect organism sensitivity to toxicants. Only one study has evaluated light as a variable (Sherberger and Buikema 1976) and it showed significant effects of photoperiod intensity and wavelength on the sensitivity of the macroinvertebrate *Daphnia* to cadmium. This increased sensitivity of *Daphnia* to the toxicant may have been mediated by changes in behavior, but other work (Buikema 1973, 1975) suggests that other physiological factors also may be operative. Fremling (1975) discussed light in his experimental design for *Hexagenia*, noting that the burrow provides semidarkness for the organism. Holt and Waters (1967) and Bishop (1969) discuss the effect of photoperiod on activity of amphipods. Light as a significant variable affecting an organism's sensitivity to toxicants has been

ignored in favor of "standardized test conditions" which may have no scientifically rational basis.

Temperature effects on growth rates, life cycle duration and general metabolism, and toxicity have been widely documented for aquatic organisms and the topic will not be discussed in detail. Examination of acute toxicity data suggests that the effects of temperature on an organism's sensitivity to toxicants may be contradictory (Cairns et al. 1978). Usually, organism sensitivity increases as temperature increases but occasionally the reverse pattern occurs. One reason for this discrepancy is that higher temperatures may facilitate toxicant degradation by the test organism or perhaps by bacterial contaminants.

Dissolved oxygen generally has an inverse effect on invertebrate sensitivity to toxicants, i.e. as dissolved oxygen drops, sensitivity increases; however, prior acclimation to low oxygen may modify this general pattern (Cairns and Scheier 1957). Oxygen deficits may increase sensitivity due to low metabolic resistance to the toxicant. In some species, low dissolved oxygen may stimulate behavioral activity designed to increase irrigation of gas exchange surfaces (Knight and Gaufin 1963, 1964) but may, at the same time, increase toxicant uptake.

Water quality affects the field distribution of organisms and their sensitivity to toxicants. Water hardness, alkalinity, Ca:Mg ratios, and pH have been discussed by many authors and the reader is referred to the "blue book" (NAS/NAE 1973) for detailed information.

Integrated Toxicity Test Design

The above discussion illustrates that there are many aspects to an organism's life history that can be incorporated into the design of a toxicity test, and the subsequent interpretation of test data. While chronic and subchronic sudies must obviously include life history information for successful completion of the experiment, acute toxicity tests still fall short of ideal design. Continuous flow experiments have increased the validity of the data collected in acute tests but many of these studies are still conducted in sterile glass containers without due consideration of proper substrate, light conditions, temperature, and water quality.

In our opinion, one of the best examples of a toxicity test design that incorporates appropriate life history information is that of Fremling (1975) for nymphs of the mayfly *Hexagenia*. Among other items, the design includes organisms of definite age, appropriate light conditions, and a proper substrate that includes a burrow that satisfies the nymph's requirements for seclusion, thigmotaxis, and water current. In this nearly natural setting, *Hexagenia* nymphs behave much as they do under field conditions, whereas in "standardized" bioassay vessels, they tend to be extremely active. Results of bioassays indicate that the nymphs are more resistant to many toxicants in the Fremling chambers than in "standardized" vessels.

Past, Present, and Future

In the foregoing discussion we have attempted to demonstrate the importance of life history information in the design of toxicity experiments using macroinvertebrates. Toxicity research has been conducted under the best practical conditions and should not be criticized haphazardly. Toxicity research has evolved considerably in the last 10 yr but one cannot avoid concluding that the "state of the art" is still in a primary stage of development.

It is easy to be critical of any research but, in all fairness, one must ask why our expertise is seemingly lagging and offer suggestions for future direction. Natural history studies have never been, and probably never will be, the most fundable research because collecting baseline data has never been considered the best use of funds. Even if life history studies were combined with pollution studies they probably would not be funded by one agency because of the applied nature of the research, nor by another agency because of the pure baseline data that would be required. Possible funding may be obtainable from certain trade organizations or industries, but such funds are usually directed towards more applied research and, currently, to litigation.

The marriage of basic and applied research has never been popular because of philosophical differences and peer pressure. The current job market was created by a combination of an overabundance of traditionally trained biologists, lack of traditional jobs in institutions of higher education, Public Law 92-500, and pressure from conservation groups, which has forced the basic and applied researchers to work together. While many scientists are not comfortable with the current arrangement, we can see the advantages of diverse interest groups working towards one goal, the protection of aquatic environments.

Regardless of the bleak future for funding, scientists need to work together to obtain life history information and to apply this information to macroinvertebrate toxicity tests. As pointed out earlier, major emphasis should be placed on culturing test animals, designing defensible acute, chronic, and subchronic tests, investigating relative sensitivity of alternate species or life stages, and considering pertinent ecological parameters that may affect test results. Currently, water quality criteria are based on very few data points that may, or may not, be adequate to protect aquatic life. Unless we pursue research in this area we will never be able to claim that we are protecting, or will protect, the aquatic biota.

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Environmental Disturbance and Life Histories: Principles and Examples[1]

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LEHMKUHL, D. M. 1979. Environmental disturbance and life histories: principles and examples. J. Fish. Res. Board Can. 36: 329–334.

While many environmental disturbances have no readily detectable effect on aquatic invertebrates in the short term, they may prevent normal reproduction and cause eventual local extinction of a species. Small temperature changes may interfere with diapause signals and prevent completion of the life cycle. Heavy metals and toxic substances may drastically reduce reproduction rates in species exposed to sublethal levels. Dissolved salts and pH affect organisms at abnormally high or low levels but most mechanisms are unknown. It is concluded that relatively little information is available on the effects of environmental disturbances on life cycles. Available information, however, is sufficient to provide evidence of many problems that require attention.

Key words: life histories, benthos, environmental disturbances, toxic substances, diapause, temperature, heavy metals

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Bien que, à court terme, plusieurs perturbations de l'environnement n'affectent pas sensiblement les invertébrés aquatiques, elles peuvent empêcher une reproduction normale et entraîner l'extinction locale d'une espèce. De faibles changements de la température peuvent interférer avec les signaux des diapauses et interrompre le déroulement complet du cycle biologique. Les métaux lourds et les substances toxiques peuvent abaisser de façon dramatique le taux de reproduction d'espèces exposées à des niveaux sublétaux. Les sels dissous et le pH affectent les organismes lorsque leurs niveaux sont anormalement élevés ou bas, mais la plupart des mécanismes nous sont inconnus. Nous arrivons à la conclusion qu'on connaît très peu les effets des perturbations de l'environnement sur les cycles biologiques. Les connaissances que nous possédons suffisent toutefois à nous indiquer que plusieurs problèmes demandent à être étudiés.

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THE purpose of this paper is to discuss the effects of various environmental disturbances on life histories of aquatic macroinvertebrates. The task has been difficult because of the breadth of the area to be covered and also the lack of research data that are clearly relevant. Some of the examples are of organisms that are not truly benthic, and the examples are far from being a review of the known data.

The relationships between life histories and environmental disturbances are usually subtle and difficult to detect. For example, a dam constructed on the Clinch River, a warmwater Alabama river, changed it into a cold-water river through release of 10°C water from the hypolimnion throughout the year (Tarzwell 1938). Almost all of the warmwater benthic fauna was eliminated. Tarzwell (1938) hoped that the river would soon be colonized by cold-water, trout stream insects and that it would change into a trout stream. He also felt that typical trout stream food organisms could be stocked in the river if natural colonization did not occur. Despite repeated attempts at stocking of trout, the Clinch River never developed into a trout stream, and according to Isom (1971), no one up to that time had *proved* why the efforts failed, although low oxygen levels in the water from the hypolimnion were held to be responsible.

My interest in the problem of the effects of environmental disturbances on life histories developed when I found a virtual absence of aquatic life in an area of the Saskatchewan River where all observations indicated that water quality was excellent (Lehmkuhl 1970, 1972, unpublished data). This river is inhabited by a unique community of mayflies, including *Anepeorus*, *Ametropus*, and *Pseudiron*, and I began searching for them in the vicinity of Saskatoon. As I moved upriver, away from the city, I expected to find a greater abundance and diversity of benthic fauna. However, collections became progressively depauperate, even though the river appeared to be physically "healthy." I suspected that Gardiner Dam, located approximately

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100 km upstream was responsible. The question was why and how.

Low dissolved oxygen concentrations could be ruled out, since the effect would hardly be expressed 50–100 km downstream from the dam. By comparing water quality in the depauperate south branch of the river with the normal north branch of the river, it was possible to eliminate many possible factors, e.g. toxins, water chemistry, pH, substrate, food, etc. It was finally apparent that a changed annual temperature profile was responsible for eliminating the organisms. For example, at least the mayfly, *Ephoron album* could not reproduce in the area influenced by the dam because it was not receiving known diapause "signals." The temperature on any given date during the year was not harmful to the organisms, but the sequence of temperatures and the overall temperature decline was responsible for the ecological death of many species (Lehmkuhl 1972; and see review by Ward 1976b).

Failure of colonization by cold-water insects in the Clinch River may be similarly explained. Cool water itself was not the only requirement for the survival of trout stream species. Life history requirements had to be met. Low dissolved oxygen concentrations may have been a problem but certainly was not the only problem involved.

This paper will document examples of other perturbations that may have disturbed the life histories of other species of aquatic invertebrates.

Nutrients and Ions

Very little precise information is available on the ecological significance and effects of nutrients and ions on aquatic life. Theoretically, the absence of essential ions would be limiting factors to the occurrence of benthic invertebrate species. For example, Nduku and Harrison (1976) found 2 mg/L Ca^{++} to be the lower limit of survival for the snail *Biomphalaria pfeifferi* when cultured in a calcium bicarbonate medium and 4 mg/L was needed for the population to thrive. Snails in calcium sulfate cultures had lower survival, indicating the importance of the bicarbonate buffer. Snails in natural waters were limited to areas with calcium concentrations of at least 5 mg/L and no snails of any species were found below 2 mg/L Ca^{++}. Adult snails would not lay eggs in natural waters with calcium concentrations under 5 mg/L, and low calcium concentrations inhibited egg production, reduced the hatching rate in eggs, and caused distorted shells in juveniles. These relationships would not be easy to detect in either field studies or short-term laboratory studies. Detailed and sophisticated life history studies were necessary.

Most life history disturbances result from excesses of nutrients and ions rather than insufficiencies. In the middle ranges of natural concentrations, I was unable to find any data to show that "normal" fluctuations have an adverse effect on aquatic invertebrates. Organisms appear to thrive over a rather wide range of concentrations (e.g. Hannon and Young 1974).

Pulses of road salt (primarily Cl^-) of up to 800 mg/L had no effect on drift patterns of aquatic insects (Crowther and Hynes 1977). However, permanent chloride concentrations of between 1000 and 2340 mg/L have caused the disappearance of many common species and an overall impoverishment of stream fauna (Crowther and Hynes 1977).

At even higher levels, such as in brackish water or inland saline lakes, most organisms are able to osmoregulate to a point, but species begin to drop out as ion concentrations increase (Wichard et al. 1973, 1975; Tones 1979; Rawson and Moore 1944).

Tones (1979) found that the beetle *Hygrotus salinarius* was able to osmoregulate in the adult stage but that haemolymph concentration in larvae was controlled by the salinity of the medium. Adults and larvae, therefore, tolerated salinity by different means. One would expect that larvae that lack the power to osmoregulate would be more sensitive than adults to abnormal changes in ion concentration.

pH

pH is widely regarded as being important in determining the distribution of organisms, but I did not encounter any data that specifically described mechanisms or vulnerable life cycle stages.

Individual species can tolerate extreme ranges of values in nature. Sprules (1975) found that in a series of acid-stressed lakes, some species of phytoplankton occurred over a range of 3.8–7, but that a large group of species dropped out at about pH 5.

Levels of pH ~4 cause a significant decrease in diversity of aquatic insects (Canton and Ward 1977). Fluctuations of pH 7 ± 1 are considered to be insignificant (Hannon and Young 1974).

Apparently more work is necessary on pH at sublethal levels, especially as it affects life cycle processes and behavior.

Heavy Metals

Heavy metals such as copper, lead, zinc, silver, and mercury are becoming increasingly recognized as severe environmental contaminants. They are highly toxic to fish, less so to invertebrates (Nehring 1976; Renzoni and Bacci 1976), and in many cases are a threat to the health of man. Winner and Farrell (1976) described the following lethal and chronic effects of copper on four species of *Daphnia*: (1) Acute toxicity ranged from 54 to 86.5 μg/L (72-h LC 50). (2) Sublethal chronic exposure to copper did not alter maturation time or frequency of reproduction in parthenogenetic females of *D. magna*, but it shortened the life span of females and reduced brood size, greatly affecting reproductive output. Copper stimulated larger broods in

some cases, but this was offset by shorter life spans of the females and thus fewer broods. In other species of *Daphnia*, sublethal concentrations reduced brood size. (3) Instantaneous rate of population growth (r) was significantly reduced by copper stress in three of the four species of *Daphnia*, and reproduction stopped in the three most sensitive species below the lethal level.

Other studies show that sublethal concentrations of heavy metals ultimately affect life histories of invertebrates. Test solutions of $\frac{1}{10}$–$\frac{1}{200}$ of the known lethal dose of copper sulfate caused significant metabolic disorders in the snail *B. alexandrina* (Ishak and Mohamed 1975). While this paper does not directly discuss life histories, it seems obvious that low levels of copper sulfate would drastically affect reproduction because of apparently irreversible physiological damage to the organism.

Sublethal concentrations of cadmium, zinc, and chromium in lake sediments caused an avoidance reaction by larval *Chironomus tentans* (Wentsel et al. 1977). While application of these results to the field is difficult, implications of the avoidance response should be considered in future studies.

Bioaccumulation of heavy metals by many invertebrates may mean that even low concentrations of heavy metals may alter community structure by shortening life span and inhibiting reproduction. Benthic communities are probably undergoing massive perturbations under the influence of what we consider to be nonproblematic, low heavy metal concentrations.

Biocides and Other Toxins

Schober and Lampert (1976) tested sublethal effects of the herbicide Atrazin on the reproductive rates of *D. pulex* and brine shrimp (*Artemia*). In *D. pulex*, concentrations of 1 mg/L reduced cumulative reproduction by about 25%. Ten milligrams per litre was nearing the level of acute toxicity. At this concentration all animals died within 12 d and reproduction was <40% the control rate. While the mechanisms and vulnerable stages are not known, low concentrations (compared to acute toxic levels) have a striking effect on total population growth.

Sublethal concentrations or residues of pesticides may have a stimulatory effect on reproduction (e.g. Dittrich et al. 1974). Recall that at certain levels, sublethal chronic concentrations of copper stimulated reproductive rates in *D. magna*. This phenomenon, hormoligosis, is thought to result from stimulation by small quantities of a stressor. Therefore even very low sublethal chronic concentrations of toxins and biocides could drastically alter community composition by stimulating reproduction in some species or reducing reproduction rates in others. Research in this area has only begun. It would be ironic if we have created our own agricultural and forest pest problems by maintaining a stimulatory level of pesticide residues.

Insect development inhibitors are a type of pesticide consisting of juvenile hormone analogs that cause death at molting (Miura and Takahashi 1974). These materials affect the molting process of a wide range of nontarget arthropods (especially crustaceans and insects), but I found no information on the possible stimulatory effects of sublethal dosages.

Changes in Physical Parameters of Watersheds

Drastic changes in physical features such as current velocity, water level fluctuations, substrate, etc. can eliminate sensitive species while allowing tolerant ones to thrive. Some information is available from studies of newly established habitats (e.g. Williams and Hynes 1976) that indicate that insects, worms, crustaceans, and molluscs constantly invade new habitats from surrounding areas. Competition and ability to reproduce in the new habitats soon molds a new community. "Fine tuning" may occur through such processes as conditioning of water by another life stage. Growth promoting substances are produced by the snail *B. glabrata* (Thomas et al. 1975). Both growth rates and natality are higher in water that has been conditioned by the presence of adults than in water that has not. Thus, various subtle aspects of life histories (e.g. fecundity, vagility, and competitive ability) control community structure and composition in freshwater invertebrates.

Fisher and LaVoy (1972) found that water level fluctuations below a hydroelectric dam produced a freshwater "intertidal zone." The basic problem was periodic desiccation which would obviously affect immobile and vulnerable life stages. This problem has been recognized for many years (Grimås 1965). Fish food organisms and aquatic plants are drastically affected. Similar problems have been documented by Radford and Hartland-Rowe (1972) and reviewed and discussed by Ward (1976a).

Changes in current velocity and substrate act selectively on individual species and on individual life history stages. A sandy stream substrate, caused by a mining operation, formed an effective barrier to upstream movement in insect nymphs and larvae except for heavy-cased *Dicosmoecus* sp. (Leudtke and Brusven 1976). Larvae and pupae of *Pycnopsyche* spp. exhibited species specific substrate preference and behavioral sequences (Mackay 1977). Lehmkuhl and Anderson (1971) reported changes in habitat preference as nymphs of *Paraleptophlebia temporalis* matured. Kovalak (1976) found an interaction between temperature and currents that influenced positioning on brick substrates by the caddisfly *Glossosoma nigrior*. Faunal changes in areas of siltation or altered current velocity are therefore predictable. More precise studies on such relationships are needed.

Temperature

The literature suggests that no natural factor is as

important as temperature, because, while pH and nutrients appear to be tolerated by organisms over a wide range, a change in temperature of a single degree Celsius can be significant.

Britt (1962) showed that the mayfly *E. album* required a strict sequence of temperatures to allow hatching and growth to maturity. Eggs would not hatch until being warmed after exposure to 0°C. Development differed at 0 and 1.3°C, indicating the degree of sensitivity. Actual hatching is stimulated by a rise in temperature to 10–13°C.

Horsfall (1974) described a similar sequence of events for hatching and growth of the mosquito *Aedes stimulans*. Eggs experience temperatures of 20–25°C after oviposition in summer followed by 4°C or below for 6 mo. In the spring, the eggs hatch after temperatures rise to >4°C. Eggs will not hatch unless exposed to 4°C or less.

A laboratory growth study of larvae of the blackfly *Simulium venustum* is summarized in Table 1 (Mokry 1976). Combining laboratory data and field temperature observations, Mokry (1976) was able to provide a growth model for *S. venustum* (Table 2).

The leech *Helobdella stagnalis* produced two generations per year in a comparatively warm pond in British Columbia but only a single generation per year in a cooler pond in Alberta (Davies and Reynoldson 1976). Thus, increases in temperature associated with thermal pollution could easily increase the number of leeches in an aquatic ecosystem. In contrast, Aston and Brown (1975) found that reproduction in the leech *Erpobdella octoculata* was apparently regulated by day length, and the life cycle pattern was similar in five different sampling stations in a thermally polluted river.

TABLE 1. Response of blackfly larvae (*Simulium venustum* to various temperatures (Mokry 1976).

Temp (°C)	Survival (%)	Observations
5	0	— eggs hatched, no growth, 1st instar died after 10 d
10	0	— larvae developed to second instar, died after 21 d
12	0	— larvae developed to 4th instar, died after 33 d
15	10	— development completed to pupal stage, 36 d
18	15	— development completed to pupal stage, 29 d
20	16	— development completed to pupal stage, 25 d
22	20	— development completed to pupal stage, 22 d
24	5	— development completed to pupal stage, 20 d

TABLE 2. Growth model for the blackfly *Simulium venustum* based on field and laboratory data (Mokry 1976).

Generation	Month(s)	Temp	Larval duration
1st	May–June	cool spring	54 d
2nd	July	$\bar{x} \sim 18$°C	1 mo
3rd	Aug.	$\bar{x} \sim 18$°C	1 mo
4th (rare)	Sept.	cooler	variable, overwinters as eggs

Further examples of the effects of temperature on the life cycles of a variety of aquatic organisms are available. The turbellarian *Phaenocora typlops* requires temperatures below 5°C to stimulate egg development (Young 1974). Temperatures above 9°C are required to stimulate hatching. The egg resting stage was an obligate diapause rather than being initiated by environmental stimuli. Thermal pollution that did not allow temperatures to drop below 5°C in winter could exterminate the species.

The planarian *Polycelis tenuis* has a higher reproductive rate at lower temperatures than *P. nigra* which explains the wider distribution of *P. tenuis* (Lascombe et al. 1975).

There is also evidence that organisms are able to acclimate or compensate for temperature changes. Planktonic crustaceans were able to develop at the normal rate at cooler than normal temperatures (Munro and White 1975; Munro 1974). Similarly, Langford (1975) did not find a significant change in insect emergence patterns in a river warmed as much as 8 deg above normal.

Thus, a wide variety of invertebrates (arthropods, leeches, flatworms) have distinct temperature requirements, and minor alterations of temperature by thermal pollution can cause drastic effects on the animal community. This applies to extreme climates (e.g. Canada) and also to relatively mild climates (e.g. England). I concluded several years ago (Lehmkuhl 1972) that thermal regime alteration caused faunal depletion up to 100 km downstream from a hypolimnion drain reservoir, and that other factors were of secondary importance. After this review, I find no reason to change my mind about the overriding importance of temperature.

Discussion

I am left with two impressions after reviewing the literature for this paper: (1) In contrast to even 5 yr ago, when very few papers relevant to this discussion were available, we now find that much valuable information has been published. (2) Much is yet to be done. Just enough information is available to let us begin to see the outlines of this new problem. Many authors are commenting on this fact. For example, Schober and Lampert (1976) have warned that the determination of acute toxicity in pesticides has little

relevance to the determination of ultimate ecological consequences and that long-term studies involving sublethal concentrations are necessary.

Likewise, Stockner and Antia (1976) (discussing algae) warn of the dangers of confusing short-term "shock" responses with long-term "habituation" responses. They note that sometimes, after the "shock" is over, the organism may adapt and live quite well with the new disturbance. Short-term studies of acute effects may mislead in two ways: (1) they may fail to detect ecologically meaningful problems, and (2) they may direct undue attention to a brief "shock" reaction.

Cairns (1976) feels that many subtle environmental perturbations caused by heated waste water are so difficult to detect that the research community is unprepared to meet the challenge, and that frequently inappropriate data are gathered. The truth of Cairns' statement is borne out by the contents of the volume in which it appears (Cairns 1976), which consists largely of descriptive studies or the results of experiments involving acute effects. I stress, again, that acute effects have little to do with ultimate ecological consequences.

Ellis (1976) (discussing marine benthos) raises the matters of judgement and cost–benefit analysis in relation to studies of benthos. As we all know, it is usually impossible to identify all the organisms collected in samples to species. To now suggest that detailed life history or other long-term studies be made on every species is not only impossible from a practical point of view, but perhaps unnecessary from a scientific point of view. It seems that we need a new conceptual framework for benthological data that will point the way to future work.

For example, toxic materials not only cause immediate death in high concentrations, but they may have equally devastating effects in the long-term at sublethal levels. They may affect fecundity, longevity, behavior, or may cause stress-induced stimulatory effects on reproduction. The effects of altered temperature may be equally complex. Generations may be lost or gained, or there may be reproductive failure. It would be useful to compile a checklist of environmental disturbances and the types of impact that they may have on life histories to reduce the danger of overlooking important yet difficult-to-detect relationships. While the references cited in this paper could be used as a beginning checklist, its brevity and incompleteness would illustrate the amount of work yet to be done, both in the laboratory and in the library. Note, for example, that while ions and pH are routinely measured, the significance of fluctuations around normal readings are obscure. After such a checklist is expanded and refined, it would be possible to quickly identify potential problems, determine whether or not appropriate data had already been gathered, and decide upon the research required.

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Influences of Diet on the Life Histories of Aquatic Insects[1,2]

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ANDERSON, N. H., AND K. W. CUMMINS. 1979. Influences of diet on the life histories of aquatic insects. J. Fish. Res. Board Can. 36: 335–342.

Benthic species are partitioned into functional feeding groups based on food-acquiring mechanisms. Effects of food quality on voltinism, growth rate, and size at maturity are demonstrated for representatives of gougers and shredders, collectors, and scrapers. Food quality for predators is uniformly high, but food quantity (prey density) obviously influences their life histories. A food switch from herbivory to predation, or some ingestion of animal tissues, in the later stages is a feature of the life cycle of many aquatic insects. Temperature interacts with both food quality and quantity in effects on growth as well as having a direct effect on control of metabolism. Thus further elaboration of the role of food in life history phenomena will require controlled field or laboratory studies to partition the effects of temperature and food.

Key words: aquatic insects, feeding strategies, functional groups, life histories

ANDERSON, N. H., AND K. W. CUMMINS. 1979. Influences of diet on the life histories of aquatic insects. J. Fish. Res. Board Can. 36: 335–342.

Nous avons séparé les espèces benthiques en groupes, selon le type d'alimentation fonctionnelle fondé sur les mécanismes d'acquisition de la nourriture. Chez des représentants de creuseurs et de déchireurs, de collecteurs et de racleurs, nous démontrons les effets de la qualité de la nourriture sur le voltinisme, le rythme de croissance et la taille à la maturité. Pour les prédateurs, la qualité de la nourriture est uniformément haute, mais la quantité de nourriture (densité des proies) influe évidemment sur leurs cycles biologiques. Un changement de régime, d'herbivore à prédateur, ou une certaine absorption de tissus animaux aux stades ultérieurs est une caractéristique du cycle biologique de plusieurs insectes aquatiques. Il y a interaction de la température avec la qualité aussi bien que la quantité de nourriture dans ses effets sur la croissance, de même qu'un effet direct sur le contrôle du métabolisme. Des études plus poussées sur le rôle de la nourriture dans les phénomènes du cycle biologique nécessiteront des expériences de laboratoire ou des études contrôlées sur le terrain afin de séparer les effets de la température et de la nourriture.

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THE study of trophic relations in freshwater communities reveals a bewildering array of foods available and methods of resource utilization. As Hynes (1970, p. 192) suggested "It may seem inappropriate to consider the food of invertebrates in any biotope, as it is obviously as varied as the invertebrates themselves." Because of such complexity, it seems necessary to attempt some simplification in evaluating the general role of nutrition in controlling aquatic insect life histories — primarily growth (i.e. rate and maximum size attained). The stereotyping of food habits, based on what is eaten, at the generic or family level for aquatic insects has been criticized (e.g. Resh 1976; Fuller and Stewart 1977). However, the partitioning of taxa on the basis of food-acquiring mechanisms, that is, community functional role, rather than what is eaten, has proven useful in approaching certain ecological questions (Cummins 1973, 1974; Merritt and Cummins 1978; Wiggins and Mackay 1978). This approach, which stresses partitioning of food resources on a community basis, reveals that detrital utilization by shredders (coarse particle feeders) and collectors (fine particle feeders) dominates most forested headwater streams. This is in contrast to many terrestrial systems in which the insects feed primarily on living plant tissue.

Various aspects of food (diet) as a factor influencing life histories, or life history strategies, are examined. Since field data implicating food as a causal factor usually have other possible explanations, our task is akin to completing a jigsaw puzzle with most of the pieces missing. Furthermore, the interaction of abiotic factors, especially temperature, with food quality and quantity (food per unit of environment) confounds the

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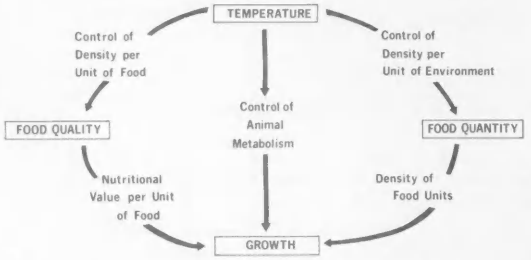

FIG. 1. Relationship between temperature and food in the control of macroinvertebrate growth.

problem (Fig. 1). A bias to lotic examples is evident both in the experimental data presented and literature cited because our research programs are directed to stream studies.

Food Resources of Aquatic Insects

The range of organic materials potentially available as foods for aquatic insects extends from the highly refractory to the readily assimilable. The relative nutritional gradient is perhaps: (1) wood; (2) terrestrial leaf litter; (3) fine particulate organic matter (FPOM); (4) decomposing vascular hydrophytes and filamentous algae; (5) living algae, especially diatoms; and (6) animal tissues. Considerable evidence has accumulated (e.g. Bärlocher and Kendrick 1973a, b) that the microbial flora associated with categories 1–4 is the primary source of nutrition for aquatic insects. Monk (1976) demonstrated a weak cellulase activity in gut extracts of several aquatic insects but found no correlation between the occurrence of cellulase and the abundance of cellulose in the diet. However, *Tipula* and other shredders have been shown to have hind gut symbionts that may be instrumental in the assimilation of products of cellulose degradation (Meitz 1975).

Gougers and Shredders

These functional groups encompass those species that feed on coarse particulate organic matter (CPOM) (food categories 1 and 2) and reduce the particle size by chewing-gouging and mining wood, and skeletonizing leaf litter. Woody detritus, the most refractory material in aquatic habitats, has a processing time of at least decades. In water, microbial degradation of wood occurs largely on exposed surfaces (Anderson and Sedell 1979). Initially food is available to invertebrates only through gouging at the surface, but when tissue softens, the inner tissues are mined. Although wood debris offers an extremely nitrogen-poor diet (C to N ratio 300–500:1), in western coniferous forests it supports a considerable fauna (Anderson et al. 1978). Life-history strategies suggested for species that exploit wood as a food source were (1) long life cycles with low metabolic activity; (2) high ingestion

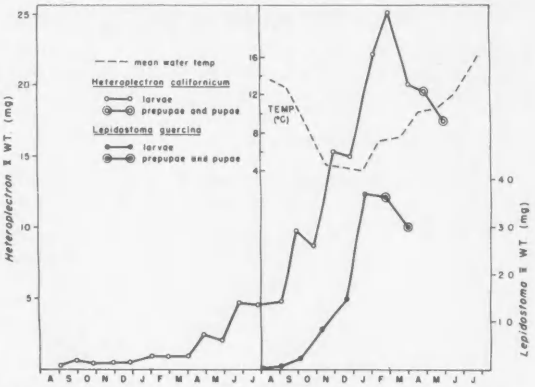
mean water temp
Heteroplectron californicum
larvae
prepupae and pupae
Lepidostoma quercina
larvae
prepupae and pupae
TEMP (°C)
Heteroplectron X WT (mg)
Lepidostoma X WT (mg)
A S O N D J F M A M J J A S O N D J F M A M J J

FIG. 2. Life cycles of the wood gouger *Heteroplectron californicum* and the leaf shredder *Lepidostoma quercina*, expressed as mean individual weight at each sample interval at Berry Creek, Benton Co., Oreg. Water temperature is given as mean monthly temperature.

rates to provide sufficient assimilative gut contact with the microbial flora to meet the animal's nutrient requirements; (3) supplemental feeding on higher quality food (especially the periphyton film); or (4) some combination of the above.

Examples of xylophages include the elmid beetle, *Lara avara*, the calamoceratid caddisfly, *Heteroplectron californicum*, the craneflies, *Lipsothrix nigrilinea* and *L. fenderi*, and midges of the genus *Brillia*. Life cycle studies of the dipterans are incomplete. *Lara avara* and *H. californicum* both grow slowly; the former probably requires 3 yr or more to complete development and the latter has a 2-yr life cycle. Microbial symbionts capable of digesting cellulose have not been demonstrated in the hind guts of either species.

The growth pattern of *H. californicum* is compared with that of a typical leaf shredder, *Lepidostoma quercina*, in the same stream (Fig. 2). The major growth period for both species is from September to February when water temperature ranges from about 12 to 4°C. *Lepidostoma quercina* is univoltine, with an instantaneous growth rate (IGR) of $2.7\% \cdot d^{-1}$, whereas *H. californicum* has a 2-yr cycle with an IGR of $0.9\% \cdot d^{-1}$.

The degradation of deciduous leaves by shredders has received considerable attention in the last decade and was recently reviewed by Anderson and Sedell (1979). From the viewpoint of dietary effects on life histories, some salient features of the shredder function are

1. Life cycles of many shredders (e.g. *Tipula* and many caddisflies) are keyed to the autumnal pulse of leaf fall, with the major growth period occuring in the late autumn and winter.

2. Shredders selectively feed on the leaves maximally colonized (conditioned) by microorganisms, especially aquatic hyphomycete fungi. This is shown by the posi-

tive correlation between selective feeding and density of microbial flora (Bärlocher and Kendrick 1973a, b), nitrogen content (Iversen 1974), and respiration rate and ATP content per unit weight of leaf (M. Ward, R. Speaker, and K. Cummins unpublished data). Thus, the rate of leaf degradation (e.g. *Alnus*, *Tilia*, *Fraxinus*, fast; *Carya*, intermediate; *Quercus*, *Fagus* and conifers, slow) is a good predictor of shredder feeding preference.

3. Although shredders selectively feed on the best conditioned substrate, they can make an adjustment in feeding rate to maintain their growth rate.

Food Quality of *Alnus* Leaves for *Clistoronia magnifica*

Compared with many common riparian species, *Alnus* leaves are high in nitrogen, rapidly conditioned, and one of the most palatable species for benthic invertebrates (Iversen 1974; Otto 1974; Petersen and Cummins 1974; Anderson and Grafius 1975). Therefore, alder leaves have been used as a standard for comparison in short-term growth studies of various Trichoptera at Oregon State University. However, when the limnephilid *C. magnifica* was reared through the entire larval stage and compared with field collected specimens, it became apparent that laboratory-conditioned alder leaves were inadequate to produce normal growth. A diet including a supplement of wheat grains or enchytraeid worms in addition to alder leaves has enabled continuous rearing of *C. magnifica* (Anderson 1976, 1978). Feeding experiments with individuals from the laboratory culture indicate that development time was at least 10 wk longer and mortality more than twice as high on alder leaves compared with a supplemented diet (Fig. 3). Mean pupal weight was only 22.65 (±1.04) mg on the nonsupplemented diet as compared with 37.90 (±2.32) mg on the leaves plus supplement.

Laboratory-conditioned leaves were compared as food with leaves incubated in a stream to test the possibility that an inferior microbial flora developed on laboratory-conditioned leaves. Conditioning time was 2–3 wk at 12–15°C in the field and at 15°C in the laboratory. Fecal production was greater with the stream-conditioned leaves than for the laboratory-conditioned leaves (Table 1), which suggests that the former were more palatable. On the evidence of their development to fifth instar and on final weights, larvae fed on field-conditioned leaves were judged to be marginally more advanced than those fed on laboratory-conditioned leaves. However, the differences in weights are not significant ($P > .05$), and both are markedly below the weights of larvae receiving a wheat supplement. Low fecal production by control larvae is attributed to higher assimilation of the wheat diet. Thus, laboratory conditioning is apparently not a major factor in reduced growth rates on the nonsupplemented detritus diet.

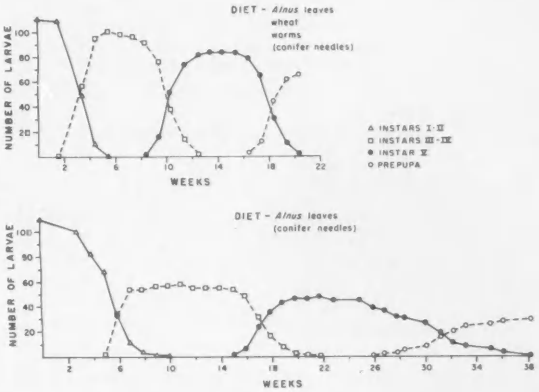

FIG. 3. Rate of development and survival of *Clistoronia magnifica* larvae reared on *Alnus* leaves compared with a control of *Alnus* plus a supplement of wheat grains and enchytraeid worms. Both series reared at 15°C, with conifer needles and sand for case material.

Higher quality food is required during the final instar when growth is rapid and fat reserves are being laid down prior to pupation. A series of 26 *C. magnifica* larvae that had been reared from week 12 to 17 on alder leaves were split into two groups after 50% of the individuals had molted to the final instar. One group was continued on alder leaves while the other received leaves and a supplement of wheat plus worms. Mean time to pupation was a further 17 wk for the alder group as opposed to only 7 wk for those that received the supplement. Even more striking were the differences in survival and pupal weight: alder, ($n = 4$), $\bar{x} = 15.0$ mg; supplement ($n = 11$), $\bar{x} = 39.8$ mg. Pupae from the stock culture (fed a supplement diet) averaged 40.1 mg. Thus, the addition of the supplement for the final 5–7 wk of the larval stage provided sufficient nutriment to allow normal weight to be regained.

Food Quality of Basswood (*Tilia*) and Hickory (*Carya*) Leaves for *Tipula abdominalis*

Recent work at the Kellogg Biological Station (M. Ward, R. Speaker, and K. Cummins unpublished data) has shown that the shredder, *T. abdominalis*, can increase its feeding rate to compensate for poor food quality and thus maintain a typical growth rate. Two levels of food quality were obtained by using hickory and basswood leaves. These were incubated with natural stream microorganisms for 9 wk at 10°C. Respiration rates were 30% higher for the basswood leaves, indicating greater microbial conditioning than for hickory and, consequently, a higher food quality. *Tipula abdominalis* larvae grew at the same rate in a 1-wk experiment when fed either type of leaf separately. The weight loss of the hickory leaves was about 30% greater than the basswood, but the efficiency of food

TABLE 1. Growth, development, and fecal production of *Clistoronia magnifica* larvae reared on laboratory-conditioned *Alnus* leaves ($n = 40$), field-conditioned *Alnus* leaves ($n = 40$), and a control of leaves plus wheat grains ($n = 20$). Larvae reared for 18 d at 15°C.

	Lab leaves	Field leaves	Control
$\bar{x}$ Initial wt (mg)	10.56±1.11[a]	10.56±1.11	10.56±1.11
$\bar{x}$ Final wt (mg)	11.40±0.77	12.24±0.63	19.75±3.67
% molted	68	82	95
Feces (mg/mg·d)	0.31	0.46	0.27

[a]95% confidence interval.

conversion to growth (relative growth rate/consumption) (Waldbauer 1968) for *T. abdominalis* larvae on basswood was twice that on hickory. That is, the larvae ingested hickory leaves more rapidly, compensating for the lower food quality.

Feeding by *T. abdominalis* larvae was minimal on both basswood and hickory leaves when the conditioning time was reduced to 2 or 3 wk. With only this type of food available many of the larvae attempted to crawl out of the experimental chambers and those that remained did not grow.

The compensatory effect of food quality in overriding direct temperature effects on shredder growth is shown in Table 2. Basswood leaves conditioned at 5°C were of higher quality than hickory leaves at 10°C. When expressed per unit of temperature time (degree days), the growth rates of *T. abdominalis* and the caddisfly *Pycnopsyche guttifer* were higher on basswood than on hickory leaves.

The above experiments suggest that the overall shredder feeding strategy is selection of the highest quality (greatest microbial biomass) food available in a given leaf accumulation, increased feeding rate if the best available is not of sufficient quality to maintain growth in the normal range, and emigration if quality or quantity is below some minimal level. Temperature control of the general metabolic rate of shredders is compensated to some extent by the temperature-mediated effects on food quality. In addition, as demonstrated for *C. magnifica* (Anderson 1976), some intake of high protein (animal) food may be required for individuals to achieve an appropriate mature weight.

Collectors

In contrast to shredders that feed on CPOM that is colonized by microbes both on the surface and throughout the matrix, collectors utilize fine particulate organic matter (FPOM) that is primarily surface-colonized by bacteria. The sources of FPOM food and its nutritional quality varies considerably. Much of it is fecal material produced by shredders and other functional groups that is recycled or "spiralled" (Wallace et al. 1977) by the stream biota. Other sources are wood and leaf fragments produced by physical abrasion and microbial maceration, senescent periphytic algae, planktonic algae, aquatic macrophyte fragments, small animals, and particles formed by the flocculation of dissolved organic matter. The organic layer on stones, described by Madsen (1972) as a matrix of bacteria, extracellular material, fungi, and organic and inorganic particles, may be used by collectors or by scrapers (see below).

Black fly larvae typify collectors that filter FPOM from the water column. Gut filling times are about 20–30 min (Ladle et al. 1972). Since the food is passed so rapidly, the nutritional value is probably derived by stripping bacteria from the refractory detritus particles. Carlsson et al. (1977) have documented a relationship between the type of food available and the life cycle of some Lapland black flies. The larvae at lake outfalls occur in denser aggregations and have faster growth than the same or other species occurring further downstream. Phytoplankton and coarse detritus ($> 2\ \mu m$) occurred in similar amounts in all reaches, so they concluded that small particles, from 2 μm down to colloidal size, were the resource that maintained the huge larval aggregations at the lake outlet. This material is produced by decomposition on the lake bottom in winter and is washed into the river during ice melt.

The influence of food quality, as indicated by particle-associated respiration rate or ATP content, on the growth of the collector-gatherer midge, *Paratendipes albimanus*, is shown in Fig. 4 and 5. All food materials were wet sieved to the same particle size range before use. The oak and hickory leaves had been conditioned

TABLE 2. Comparison of growth rates of two shredder species on high (basswood, *Tilia americana*) and medium (hickory, *Carya glabra*) quality leaf litter at different temperatures. Experiments conducted for 28 d in experimental stream channels under controlled flow and normal photoperiod conditions.

Leaf type	Mean temp (°C)	Degree days	% Loss/deg day	Respiration of leaves ppm O_2/g DW·h^{-1}	Relative growth rate (% body wt) *Tipula abdominalis* per day	*Tipula abdominalis* per deg day[a]	*Pycnopsyche guttifer* per day	*Pycnopsyche guttifer* per deg day[a]
Basswood	5	147	0.38	0.022	2.22	0.424	4.70	0.895
Hickory	10	282	0.27	0.013	3.51	0.348	5.19	0.515

[a]The factoring out of temperature in these calculations assumes that growth is very low at 0°C.

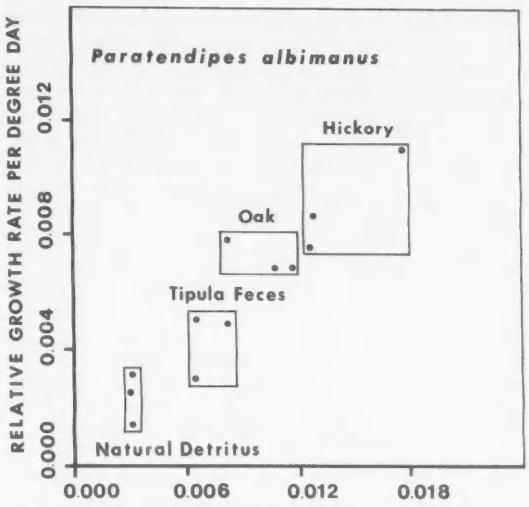

FIG. 4. Relative growth rate (Waldbauer 1968) of *Paratendipes albimanus* fed four diets (all sieved to the same particle size) compared at three temperatures (10, 15, 20°C) on the basis of substrate respiration rate ($\mu LO_2 \cdot mg\ AFDW^{-1} \cdot h^{-1} \cdot °C^{-1}$). Modified from Ward and Cummins (1978).

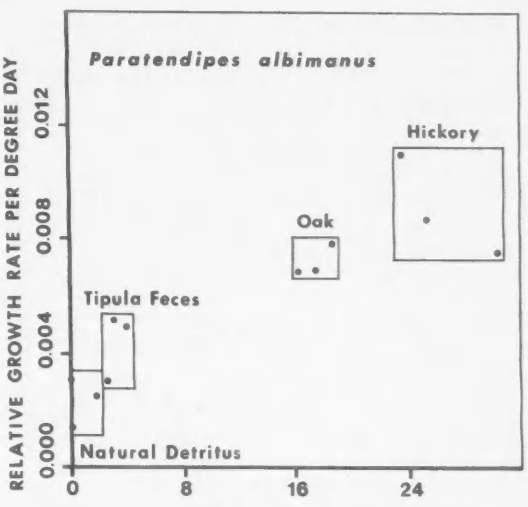

FIG. 5. Relative growth rate of *Paratendipes albimanus* fed four diets compared with substrate ATP content as an index of microbial biomass (μM ATP/mg AFDW). See Fig. 4 caption for additional details.

in aerated batch cultures with aquatic hyphomycete fungi inocula for 2 wk. The leaves were dried, ground, and wet sieved to the appropriate size range. The experiments were conducted at three temperatures (10, 15, and 20°C). Each of the three points for each food type represents a temperature in Fig. 4 and 5. Although in all cases the higher temperature produced the highest growth rate on a given food, it is clear that food quality outweighed the direct effect of temperature on larval growth.

Scrapers

This functional group is typified by glossosomatid caddisflies, representatives of the baetid, heptageneid, and ephemerellid mayflies, and psephenid beetle larvae (Merritt and Cummins 1978). Scrapers are dependent primarily on autochthonous production as a food resource but their mode of feeding also results in ingestion of detritus, as well as the organic layer on stones (Madsen 1972). The nutritional content of live algal cells is high; Cummins and Wuycheck (1971) report differences of several hundred calories per gram between diatoms and detritus.

Previous studies indicated that *Glossosoma nigrior* from first-order streams were much smaller than those in a third-order stream (Cummins 1973, 1975). Gut content analysis revealed that larvae in the small stream consumed more detritus whereas those in the third-order stream fed predominantly on diatoms. The interaction of temperature and food on growth of *G. nigrior* is shown in Table 3. The ratio of gross primary production to community respiration (P/R) is a reflection of the available algal food, and the data indicate a strong relationship between P/R and the final larval (prepupal) weights.

As shown by Gose (1970), the amount of accumulated temperature can influence the number of generations of a scraper species, and it probably affects the maximum size attained by individuals in a given cohort. There was a 20% greater accumulation of day degrees in the third-order stream, which is undoubtedly a con-

TABLE 3. Dry weights of *Glossosoma nigrior* prepupae from six sites in the Augusta Creek watershed, Kalamazoo and Barry Co., Mich. (collected Nov. 11–12, 1977).

Stream site	Stream order	Degree days[a]	P/R[b]	*N*	Mean dry wt (mg)	C.V. (%)
Smith Cr.	1	2398	0.39	28	1.512	13.1
B. Ave.	1	2443	0.73	32	1.666	12.3
Upper 43rd	2	2863	1.76	34	4.018	17.7
Lower 43rd	3	3006	—	27	4.638	21.6
C Ave.	3	—[c]	—	40	3.749	17.3
Nagel's	3	2811	1.70	26	4.507	11.5

[a]Based on mean weekly temperatures.
[b]Gross primary production community respiration measured over 24-h period in circulating chambers (D. L. King and K. W. Cummins unpublished data).
[c]Temperature regime approximately the same as Nagel's.

tributing factor to the larger size of the *G. nigrior* larvae, but the data also implicate food quality (e.g. ratio of algal cells to detritus) and quantity (e.g. density of algae per unit of rock surface).

Predators

Predators, that is, species that feed on live prey by active capture, have high assimilation efficiencies (75–85%, Heiman and Knight 1975). Although food quality is uniformly high, the quantity (prey density) can vary significantly. Thus, effects of food on the life cycles of predators occur as density effects, both in numbers or biomass of predators, or differences in generation time.

Azam and Anderson (1969) compared populations of *Sialis californica* in a stream section where chironomid populations were high due to enrichment with sucrose and urea, with an upstream nonenriched section. *Sialis californica* was univoltime in the enriched area whereas a portion of the population required 2 yr in the control section. Azam (1969) was able to simulate the growth patterns that resulted in 1- and 2-yr life cycles by using different levels of rations in feeding experiments.

Johnson (1973) demonstrated with damselfly larvae that searching movement increases as prey density falls from high to low, but at very low prey densities the larvae remain stationary and again wait for prey, presumably because of the high metabolic cost of increased searching.

Inter- and intraspecific competition and territoriality were important factors affecting the life cycle of the damselfly, *Pyrrhosoma nymphula,* in Macan's (1977) 20-yr study of trophic relations in Hodson's Tarn, England. Larvae of *P. nymphula* feed primarily on planktonic Crustacea as a "sit and wait" type of predator. When prey are scarce, *P. nymphula* can fast for long periods. They may take two full summers to complete development if they do not obtain enough food to complete it in one. When predator density was high, there were two size-groups at the end of the summer. Macan suggests that the large larvae had obtained vantage points where food was frequently within reach, while the small larvae were relegated to inferior feeding sites. He proposed that the starvelings would eventually die unless good feeding sites became vacant. When fish were in the pond, their predation on large larvae would lead to vacancies in optimal feeding sites which would then be filled by small larvae. Macan postulates a self-regulating population mechanism whereby a substantial consumption of large larvae by fish does not greatly reduce the numbers of damselflies reaching maturity because the loss of large larvae allows the small larvae to exploit the copepod population.

Resh (1976) demonstrated that food quality affected the life cycle of the sponge-feeding leptocerid caddisfly, *Ceraclea transversa.* Larvae that occur during the summer feed on the sponge, *Spongilla lacustris,* and reach the nonfeeding prepupal stage is early autumn at the time the colonial sponge declines and produces gemmules. Larvae that emerge later in the summer also feed on sponge but only reach the third or fourth instar before the sponges become inedible due to gemmulation. Thus, they are forced to shift to a detritus diet and growth is suspended until spring when there is a return to sponge feeding. Larvae of this cohort are significantly smaller than those that complete growth before overwintering. Resh indicates that the two cohorts operate as independent functional units in the larval stages, but presumably there is some gene flow between the two populations. Both cohorts have a univoltine life cycle so the differences in food quality do not greatly affect the duration. However, larvae of the second cohort are actively feeding for longer, which exposes them to more environmental hazards, and the smaller size of adults indicates a lower fecundity.

A shift from algal or detrital feeding to predation has been demonstrated in later larval stages for several stoneflies and caddisflies (Siegfried and Knight 1976; Fuller and Stewart 1977; Winterbourn 1971; Wiggins 1977). The more unusual switch from predation to heavy algal feeding was reported for the stoneflies, *Stenoperla prasina* (Winterbourn 1974) and *Acroneuria californica* (Siegfried and Knight 1976); in both instances this was apparently a response to an alternative food that was available for a limited period. As pointed out previously, the ingestion of animal tissue in the later stages of the growth cycle may be an important feature of the life cycle of many species of aquatic insects.

Discussion

Differences in growth rate directly affect duration of life cyles (i.e. voltinism), size attained at maturity (and therefore fecundity, which is positively correlated with female size), and survivorship. Temperature and food quality and quantity are control parameters with significant interactions on rate of growth. Thus isolation of the role of food in life histories is difficult to achieve without controlled laboratory or field experiments. As pointed out by Pritchard (1979), the duration and timing of aquatic insects life cycles are more indeterminate than is usually suggested. He cites examples of cohort splitting, where individuals of the same cohort may have 1, 2-, or even 3-yr life cycles. Detrimental effects of a poor diet will be most apparent with multivoltine species because those that have a univoltine (or longer) cycle usually have a period of arrested development of variable length that can be shortened to increase the feeding interval (Pritchard 1976).

The recent work of Sweeney and Vannote (1978) has convincingly shown that adult body size and fecundity of a number of aquatic insects depend largely on thermal conditions during the larval period. Changes of 2 or 3 deg Celsius either warmer or cooler than the optimum temperature regime can affect both the rate

and duration of larval growth to the extent that adult size is significantly reduced. Thus, in any study of growth, it is important to separate as far as possible the direct (animal metabolism) and indirect (food quality and quantity) effects of temperature.

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Benthic Life Histories: Summary and Future Needs[1,2]

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WATERS, T. F. 1979. Benthic life histories: summary and future needs. J. Fish. Res. Board Can. 36: 342–345.

The symposium indicated many ways in which greater knowledge of benthic life histories can be used to develop and improve techniques such as sampling, taxonomic methods, and bioassays. Benthic organisms' diet and physical environment, factors variable in nature, were shown to be capable of modifying certain life history features such as growth rate and voltinism. The lack of accumulated life history data and the need to tailor sampling schedules to life history events were commonly identified elements in the symposium. Future research needs included (1) basic data on benthic life history, (2) improved taxonomy of immature benthic invertebrates, and (3) understanding the entire life history of an organism in relation to the seasonal progression of its environment. Management implications of benthic life history information included more applicable data from long-term bioassays on all life history stages, and improved management of stream fisheries through habitat alteration to manipulate benthic production.

Key words: life history, benthos, symposium

WATERS, T. F. 1979. Benthic life histories: summary and future needs. J. Fish. Res. Board Can. 36: 342–345.

Au cours du colloque, on a indiqué plusieurs façons d'utiliser de meilleures informations sur le cycle biologique d'organismes benthiques afin de mettre au point et améliorer les techniques telles que l'échantillonnage, les méthodes taxonomiques et les analyses biologiques. On a démontré que le régime alimentaire et le milieu physique des organismes benthiques, facteurs variables dans la nature, peuvent modifier certaines caractéristiques du cycle biologique, telles que le rythme de croissance et le voltinisme. Parmi les points communément identifiés au cours du colloque, on note le manque de données accumulées sur les cycles biologiques et le besoin d'échelonner l'échantillonnage selon les événements de ces cycles. Parmi les besoins futurs en recherche, on compte: (1) les données de base sur le cycle biologique benthique, (2) une taxonomie améliorée des invertébrés benthiques immatures et (3) la compréhension du cycle biologique complet d'un organisme en relation avec l'évolution saisonnière de son milieu. Pour ce qui est de la manière dont les gestionnaires peuvent utiliser les connaissances sur les cycles biologiques benthiques, on note des résultats plus facilement applicables d'analyses biologiques à long terme sur tous les stades du cycle biologique. On note aussi une meilleure gestion des pêches fluviales par altération de l'habitat et manipulation de la production de benthos.

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THERE are many features of a particular species' existence that may be considered to fall within the purview of life history. Oliver defines life history as "reproduction and the events leading to survival." As such, the life history of a species includes matters that relate basically to the *history of its life* — its method of birth; its growth pattern and rate; its feeding, locomotory, and social behavior; its length of life; its selected habitat; its response to environmental factors; its mode of reproduction. To these could also be added, its form of death. A particular combination of these features should be unique to a species within a habitat type. The contributions to this symposium have been concerned, therefore, with subjects such as voltinism, habitat requirements, changes in habitat requirements through the life cycle, and modes of reproduction.

Six topics have been included in this symposium; but these six can be grouped into two quite different categories. First, four topics (sampling insects [Resh], sampling non-insectan invertebrates [Malley], taxonomy [Oliver], and bioassay [Buikema and Benfield]) were approached from the standpoint of the effect of life history features on the techniques (e.g. how growth patterns or developmental stages affect the schedule of a sampling program; how different behavior patterns of two morphologically similar species can lead the taxonomist to identify and separate species; how additional life history knowledge can lead to an integrated bioassay approach and data on the effect of toxicants on all life history stages). Resh also touched on the significance of life history features to the calculation of secondary production.

Second, the other topics (diet [Anderson and Cummins] and habitat disturbance [Lehmkuhl]) were considered environmental factors that can themselves modify life history features.

Common Elements

A number of life history aspects appear commonly enough in the symposium to warrant special attention. Predominant among these is the simple lack of accumulated basic data on life histories of benthic invertebrates. Needed is a "data bank" of information categorized by taxa, available to both researchers and resource managers. There are probably several reasons why such information has been slow to develop: (1) lack of funding by granting foundations, probably because of the basic or elementary nature of the work — such research does not deal with the more glamorous and exciting investigations into new ecological theory, ecosystem modeling, etc.; (2) lack of support by governmental natural resource agencies which must place priorities on management (often crisis-based) applications, and in which the use of tax or license monies almost always dictates strong public scrutiny combined with demands for quick solutions to problems; (3) the greatest applied demand for life history data is from water pollution control biologists or fishery managers who have neither the expertise nor agency support for conducting basic life history studies of their own.

A second common element is the real need to tailor sampling schedules — for whatever purpose, but probably mainly for determination of standing stock, densities, growth rates, etc. — to the progression of life history events of the organisms being studied and to the specific objective of the sampling. For example, if the objective is to determine the initial density of an insect generation, then sampling should intensify in the early period of that generation so that times of greatest density, between hatching and mortality of first instars, would not be missed. When the objective is to study growth patterns, more frequent sampling should be conducted during the life of a cohort when growth is high. This would usually mean more frequent sampling in the early life of a cohort, while sampling in the latter part might be drastically reduced without sacrificing precision. Up to now, almost no attention has been paid to these problems, whereas the usual sampling on a "once-per-month" schedule has been almost universal.

A third common element in the symposium has been the emphasis on the plasticity of certain life history features. This was demonstrated particularly well by the presentations indicating the effect of environmental factors on life history. It has been well known, for example, that water temperature may exert control on growth rate and length of life cycle, and consequently on voltinism, particularly with mayflies. But the lack of a normal progression of environmental events, including water temperature changes, may not only change the growth rate or voltinism but also so disrupt the normal progression of other critical life history events that the population may not be able to complete its life cycle and will be extirpated. Additionally, and what apparently has not been so widely known is that life history features depend heavily on the quality and quantity of food. Differences in quality (caloric concentration, protein levels) in allochthonous detritus, depending on riparian bush or tree species, may play determinant roles in such life history features as growth rate and pattern, and number of generations per year, even overriding water temperature effects. Obviously, certain life history features are remarkably impressionable in their response to environmental fluctuations. A host of other variables, photoperiod, light intensity, oxygen concentration, social aspects of crowding, and others, remain to be investigated for similar effects on life history features.

Future Research Needs

As outlined above, there is a great need for the accumulation of basic life history data; this includes variation of life history features, such as voltinism, that may be expected under different conditions of temperature and food. An appreciation is needed for support of

basic life history studies, and perhaps this symposium will assist in stimulating higher priorities for life history research proposals within granting foundations. Now is an opportune time for a review article on life histories of benthic invertebrates, to summarize our knowledge and identify current needs.

Secondly, there is a great need in taxonomy to improve identification of benthic invertebrate species. In this context, the *species* is emphasized not only for the greater precision that a species identification lends to a piece of research, but more importantly because of the possible differences in life history among two or more species, and the many connotations that different life histories impart to an ecological investigation. Two similar species that may be unidentifiable in the immature stages (usually the stages of primary concern to a benthologist) may have completely different temporal distributions, different voltinism, different minimum and maximum sizes. All of these life history features are vitally important to the ecologist attempting to estimate production in relation to environment or to the pollution biologist determining whether environmental damage has occurred or will probably occur in a water body impacted by cultural changes. The critical element is the diversity of life history schemes employed by benthos, because a diversity of taxa means little unless it can be interpreted in terms of function. However, as Oliver points out, the life history relationship in taxonomy is a mutualistic one: whereas the taxonomist may provide the benthologist with the means to identify his specimens, life history data obtained by the ecologist may also enable the taxonomist to identify his material through a functional or behavioral analysis. The need here is two-way: cooperation and mutualism between the taxonomist and the ecologist in arriving at a taxonomy that depends on life histories of the organisms involved.

A third important need for future research is the development of culture procedures and facilities for aquatic invertebrates that take into account the life history needs of the experimental organisms. The literature, and the experience of many investigators, is replete with failures to maintain in the laboratory populations of aquatic invertebrates through their entire life cycle. Undoubtedly these failures are the result of the lack of provision of environmental requirements for the completion of all life history stages; but clearly we do not yet understand these requirements sufficiently, and thus critical experiments cannot be run with the degree of reliability and reproducibility that is called for by the demands of today's environmental problems.

Fourth, we need to understand the life history of a benthic invertebrate in its total context. Lehmkuhl points out that while an environmental disturbance (damming of a river) did not change an environmental factor to a lethal level (at least as measured by short-term tests), the progression of environmental events was sufficiently disturbed to disrupt life history events, leading to disastrous effects on the benthic population. On the other hand, an environmental disturbance (again, river damming) has had, in some cases, a positive effect on productivity of the benthos and fisheries, probably also as a result of changed life histories. In either case — loss or again in productivity — the taxonomic composition of the benthic community probably changes as a result of changed conditions affecting life histories, and these changes, largely unknown, remain a fertile field for investigation.

Management Implications

Water pollution control and fisheries management are two major areas of natural resource administration that will most probably benefit from increased knowledge of and attention to benthic life history information.

For definitive water quality standards that are intended to protect aquatic life, long-term bioassay results are required to identify sublethal effects on invertebrate life histories. Buikema and Benfield emphasize that it is necessary to know the effect of the *toxicant* rather than the effect of the *test conditions*, i.e. use of an integrated approach intended to probe the impact of a toxicant on all life history stages. The lack of such information obviously frustrates the investigator searching for the reason behind the loss of invertebrate populations below a river dam, as Lehmkuhl describes, even though in this case a toxicant was not involved. The regulation of dams with respect to water temperature is not a common practice, except in some cases to provide a cold-water, low-level discharge that creates a new trout fishery in the tailwaters. But simply discharging cold or warm water for a particular fishery may or may not be successful, whereas success may depend on the effect of thermal changes on the invertebrate populations, expressed via their life history responses. As indicated above, this subject remains a fertile field for investigation, not only as an interesting and vital topic in benthic research, but also as one that may lead to improved management of fishery resources affected by river dams, as well as other thermal disturbances (e.g. discharge of cooling water from power plants and other industries).

A second area of management possibility lies in the manipulation of riparian vegetation along streams with valuable fisheries. Stream fisheries management has been concerned with riparian vegetation for a long time and for a variety of reasons: removal of trees to reduce transpiration and thereby improve groundwater supplies to the stream; maintaining stream cover to provide shade (and thus cooling) and a source of terrestrial invertebrates as fish food; removal of canopy to allow sunlight to reach the stream and increase photosynthesis; removal of canopy to provide sunlight on streambanks and the development of strong turf which protects banks from erosion; maintaining deciduous vegetation to provide allochthonous detritus as a food

base for invertebrate populations; even removal of vegetation to allow for the back cast of the fly-fishing angler! Obviously, some priorities must be set and choices made, and these depend on a number of factors such as the fish species involved and their preferred foods, the fertility of the water, initial temperature and groundwater conditions, and the type and intensity of angling use. Anderson and Cummins have introduced the factor of the *quality* of allochthonous detritus input to the stream, providing data to show that quality of the invertebrates' diet affects their life histories. This suggests the possibility of manipulation of riparian vegetation to favor certain benthic species that will provide food for fish.

The old concept of basing fish management procedures on benthic standing stock has been largely discarded because it has been recognized that simple standing stock data often bear little relationship to the stream's capacity for fish production. However, rather than being limited to standing stock data only, the older concept may have a renewed significance when revised with benthic production rates computed by modern methods. However, the computation of production depends very heavily on sound life history information for the benthos, or at least those groups within the benthos that are primarily utilized as food by fish. Obviously, fisheries management based on benthic production will depend on a solid data base of benthic life history.

Conclusion

Several papers in the symposium point out the inaccuracies of quantitative data collected in sampling strategies that were based on faulty life history information or, more commonly, did not take specific life history information into account at all. These now lead to the inevitable although uncomfortable conclusion that many quantitative data collected in the past are inaccurate and invalid. The emphasis recently placed on the abundance of benthic organisms in the hyporheic zone of streams is a clear case in point.

This may seem to be a pessimistic point of view, at first glance, but the problem need not be viewed pessimistically any more than any other scientific problem that opens up a new field of investigation or that calls for a different approach to an old one. Rather, benthologists as a group should feel much gratified, as a result of this symposium, that at long last they are facing up to a problem that has been with them for a long time.

The symposium, typically, was composed of several participants contributing from their particular viewpoints and subjects. Thus it lacks the coherence of one mind viewing the subject of benthic life history as a whole and the role of that subject in the broader one of benthic science, or even of limnological science. Yet enough coherence, enough commonality, is evident to point out a need for the broader analysis.

Several (no doubt many) specific items were missed. For example, while Anderson and Cummins pointed out the influence of the quality of diet upon stream organisms, a similar situation probably exists in the lentic environment as well (e.g. the relative dietary importance of algae and detritus on lake bottoms). The types of disturbances in rivers discussed by Lehmkuhl also occur in lakes. Dispersal (e.g. drift in streams, vertical migrations through differential currents in lakes) as a factor affecting life history was not considered. The symposium did not examine the doubtless significant interrelationships between benthic invertebrates and the life histories of other organisms (e.g. algae and other green plants, fungi and bacteria, vertebrates). The list could be extended.

Clearly, there is a need for the development of a conceptual framework for benthic ecology within which life history may play the key role. Indeed, life history — rather than productivity (as Paul Welch stated many years ago) — may be the most useful base for limnological analysis. Obviously, we are well on the way to recognizing the importance of adequate life history information in all quantitative ecological research.

It is, perhaps, this recognition that is the major result of the symposium.

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Optimal survey design: lessons from a stratified random sample of macrobenthos
W. Cuff and N. Coleman

Temperature selection and estimated thermal acclimation by rainbow trout (*Salmo gairdneri*) in a thermal plume **S. A. Spigarelli and M. M. Thommes**

Two electivity indices for feeding with special reference to zooplankton grazing
H. A. Vanderploeg and D. Scavia

Method, validity, and variability in the age determination of yellowtail rockfish (*Sebastes flavidus*), using otoliths **D. K. Kimura, R. R. Mandapat, and S. L. Oxford**

Analysis of the British Columbia salmon purse-seine fleet: dynamics of movement
R. Hilborn and M. Ledbetter

Prey selection by drift-feeding brown trout (*Salmo trutta*) **N. H. Ringler**

Sensitivity analysis of two harp seal (*Pagophilus groenlandicus*) population models
R. K. Mohn

Correlations between *Daphnia magna* and fathead minnow (*Pimephales promelas*) chronic toxicity values for several classes of test substances **A. W. Maki**

World distribution of Atlantic salmon, *Salmo salar* **H. R. MacCrimmon and B. L. Gots**

Notes

A culture technique using marine fish kidney to obtain chromosomes
E. H. Park and S. D. Park

Pygmy whitefish, *Prosopium coulteri*, in three lakes of the Copper River System in Alaska
F. H. Bird and K. Roberson

Indices of food type preference by a predator **J. E. Paloheimo**

In vitro maintenance of amoebocytes from the American oyster (*Crassostrea virginica*)
F. Brewster and B. L. Nicholson

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ANNOUNCEMENTS/AVIS

Symposium: Marine Chemistry into the 80s

The Vancouver Island Section and the Analytical Chemistry Division of the Canadian Institute of Chemistry in cooperation with the Institute of Ocean Sciences, Sidney, B.C., the University of Victoria, and the Province of British Columbia are sponsoring a 2-day symposium devoted to discussion of the directions for Marine Chemistry in the coming decade.

The symposium will be held on May 31 and June 1, 1979 at the University of Victoria. The program includes four plenary speakers and 12 guest speakers. Themes for each half-day session will be introduced by the four plenary speakers: Hydrocarbons by R. Hites, Massachusetts Institute of Technology; Biochemistry and Nutrients by P. Hochachka, University of British Columbia; Ultra-trace Analysis by C. Patterson, California Institute of Technology; and Pollution by H. Windom, Skidaway Institute. Guest speakers include: S. Berman, W. Giger, K. Keizer, R. Lee, R. Pocklington, B. Simoneit, A. Zirino, V. Zitko.

A salmon barbecue dinner and tour at the Institute of Ocean Sciences is planned for the evening of May 31. Guest speaker for this event will be Mike Waldichuk, Pacific Environment Institute.

Those wishing further information and registration forms are asked to contact *Dr J. A. J. Thompson, c/o Institute of Ocean Sciences, P.O. Box 6000, Sidney, B.C., V8L 4B2. Phone (604) 656-8408.*

Colloque: La chimie de la mer dans les anneés 80

La Section de l'île Vancouver et la Division de chimie analytique de l'Institut canadien de chimie, en coopération avec l'Institut des sciences océaniques, Sidney, C.-B., l'Université de Victoria et la province de la Colombie-Britannique, organisent un colloque de 2 jours au cours duquel on discutera de l'orientation que prendra la chimie de la mer durant la prochaine décennie.

Le colloque aura lieu les 31 mai et 1er juin 1979 à l'Université de Victoria. Le programme comprend quatre conférenciers aux séances plénières et 12 conférenciers invités. Les quatre conférenciers des séances plénières exposeront le thème de chaque séance d'une demi-journée: les hydrocarbures, par R. Hites, Massachusetts Institute of Technology; la biochimie et les éléments nutritifs, par P. Hochachka, Université de la Colombie-Britannique; l'analyse des ultraoligo-éléments, par H. Windom, Institut Skidaway. Parmi les conférenciers ivinités, il y aura: S. Berman, W. Giger, K. Keizer, R. Lee, R. Pocklington, B. Simoneit, A. Zirino, V. Zitko.

Le soir du 31 mai, il y aura diner au saumon barbecue et une visite de l'Institut des sciences océaniques. Le conférencier invité pour l'occasion sera Mike Waldichuck, de l'Institut de l'environnement du Pacifique.

Pour plus amples renseignements et formules d'enregistrement, on est prié de s'adresser au *Dr J. A. J. Thompson, a/s Institute des sciences océaniques, Case postale 6000, Sidney, C.-B., V8L 4B2. Téléphone (604) 656-8408.*

Report on 14th General Meeting of SCOR and Request for Topics for 1980 General Meeting

The Scientific Committee on Oceanic Research (SCOR) of the International Council of Scientific Unions met November 13–17, 1978, in Brest, France, at the Centre Océanologique de Bretagne, and was attended by three Canadian delegates: R. W. Stewart, C. Garrett, and D. Ellis. SCOR is a means of interdisciplinary and international contact for oceanographers and provides a channel for generating joint action, e.g. SCOR establishes working groups on matters requiring agreement, such as salinity definitions, oceanographic tables, sampling methodology. SCOR functions as an advisory body to a variety of United Nations agencies. SCOR is based on National Committees and serves as a channel of communication between United Nations agencies and national groups of oceanographers. This channel of communication can be useful to the individual scientist wishing to relate his work to broader scale oceanographic effort or to resolve difficulties fundamental to his discipline and requiring international agreement.

At the 1978 14th General Meeting there was a 2-day review of papers and discussions of oceanic fronts. These ranged over the scale of the phenomena (ocean regional fronts, shelf and-estuarine), their various causes and the geological and biological (including benthic) responses of the marine ecosystem There was mention also of analogous phenomena related to ice, estuarine salt-wedges and turbidity currents. The papers are expected to be published in *Progress in Oceanography*. Conceptual approaches to fronts may lead to applications to less intensive environmental gradients.

The business meeting was given partly to the need to redefine SCOR's role as an advisory body. Should it restrict itself largely to deep-sea and theoretical matters, or accept

Rapport de la 14e réunion générale du CSRO et invitation à soumettre des thèmes de discussion pour la réunion générale de 1980

Le Comité scientifique pour les recherches océaniques (CSRO) du Conseil international des unions scientifiques s'est réuni du 13 au 17 novembre 1978 à Brest, France, au Centre océanologique de Bretagne. Trois délégués canadiens y assistèrent: R. W. Stewart, C. Garrett et D. Ellis. Le CSRO fournit aux océanographes une occasion d'établir des contacts interdisciplinaires et internationaux, et est un instrument permettant d'amorcer une action conjointe, e.g. le CSRO met sur pied des groupes de travail sur des sujets nécessitant un accord, tels que définitions de la salinité, tables océanographiques, méthodologie de l'échantillonnage. Le CSRO est un corps consultatif auprès de divers organismes des Nations Unies. Le CSRO est fondé sur des comités nationaux et sert de voie de communication entre les organismes des Nations Unies et des groupes nationaux d'océanographes. Cette voie de communication peut être utile au scientifique individuel désirant établir un rapport entre son travail et l'effort océanographique de plus grande envergure, ou résoudre certaines difficultés particulières à sa discipline et nécessitant un accord international.

Au cours de la 14e réunion générale de 1978, il y eut 2 journées consacrées à l'analyse de travaux et aux discussions des fronts océaniques. Ces dernières couvrirent la gamme des phénomènes (fronts régionaux océaniques, sur les plateaux continentaux et dans les estuaires), leurs diverses causes et les réponses géologiques et biologiques (y compris du benthos) de l'écosystème marin. On fit aussi mention de phénomènes analogues se rattachant à la glace, aux coins d'eau salée dans

responsibility for more applied matters in turn largely restricted to shelf seas?

The Canadian National Committee seeks input from the Canadian oceanographic community on topics requiring international and interdisciplinary agreement. For the moment I am stressing the need to establish protocols for measuring responses of benthic faunas over periods of time and utilising existing survey results based on outdated instruments and concepts from as far back as the earliest deep-sea expeditions. In addition I have proposed as a topic for review "Rehabilitation of marine ecosystems" as one with an interdisciplinary basis, and of international scale (in the sense of cleanup of the ocean as well as shelf contamination).

I ask biological oceanographers and marine biologists with opinions on these and other relevant matters to write to me (*Derek Ellis, Biology Department, University of Victoria, Victoria, B.C. V8W 2Y2*); I will pass such opinions to the Canadian National Committee for SCOR for eventual transmission to the proposed 15th General Meeting at Woods Hole in 1980. Scientists in other disciplines may prefer to contact Dr R. W. Stewart, Institute of Ocean Sciences, Patricia Bay, B.C. or Dr C. Garrett, Institute of Oceanography, Dalhousie University, Halifax, N.S.

les estuaires et aux courants de turbidité. Les travaux devraient être publiés dans la revue *Progress in Oceanography*. Il se peut que des approches conceptuelles aux fronts conduisent à des applications à des gradients moins prononcés de l'environnement.

La séance de travail fut consacrée en partie au besoin de redéfinir le rôle du CSRO comme corps consultatif. Devrait-il se limiter surtout aux mers profondes et aux questions théoriques, ou s'occuper de sujets appliqués qui, à leur tour, sont en grande partie limités aux mers épicontinentales?

Le comité national canadien désirerait recevoir des commentaires de la part de la communauté océanographique canadienne sur des sujets requerrant un accord international et interdisciplinaire. Je veux ici insister sur le besoin d'établir des méthodes de mesure des réponses de faunes benthiques sur des périodes de temps et d'utiliser d'actuels résultats de relevés fondés sur des appareils et des concepts démodés, aussi loin en arrière que les premières expéditions dans les mers profondes. De plus, j'ai suggéré comme sujet à examiner «La réhabilitation des écosystèmes marins» ayant un aspect interdisciplinaire et d'envergure internationale (au sens du nettoyage de l'océan aussi bien que de la contamination du plateau continental).

Je prierais les océanographes biologistes et les spécialistes en biologie marine qui auraient des idées sur ce sujet et autres questions pertinentes de bien vouloir m'écrire (*Derek Ellis, Département de biologie, Université de Victoria, Victoria, C.-B. V8W 2Y2*). Je transmettrai leurs opinions au comité national canadien du CSRO pour transmission éventuelle à la 15e réunion générale qui se tiendra à Woods Hole en 1980. Les scientifiques spécialisés dans d'autres disciplines préféreront peut-être s'adresser au Dr R.W. Stewart, Institut des sciences océaniques, Patricia Bay, C.-B., ou au Dr C. Garrett, Institut d'océanographie, Université Dalhousie, Halifax, N.-E.

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